

# PHYLOGENETIC ANALYSIS OF SEED PLANTS AND THE ORIGIN OF ANGIOSPERMS<sup>1</sup>

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## ABSTRACT

Principles of phylogenetic analysis (cladistics) are introduced with an examination of relationships among extant genera of Gnetales. The Gnetales can be supported as a monophyletic group, with *Gnetum* and *Welwitschia* more closely related to each other than either is to *Ephedra*. Characters of the progymnosperm *Archaeopteris* and 19 extinct and extant seed plant taxa are then reviewed as a basis for a cladistic analysis of their interrelationships. The seed plant taxa included are: medullosans, cycads, *Lyginopteris*, *Cordaixylon*, *Mesoxylon*, *Lebachia*, extant conifers, *Ginkgo*, *Callistophyton*, peltasperms, glossopterids, *Caytonia*, corystosperms, Bennettitales, *Pentoxylon*, *Gnetum*, *Welwitschia*, *Ephedra*, and angiosperms. Preliminary analyses of relationships within conifers, glossopterids, and Bennettitales are also presented. Results suggest that seed plants are a monophyletic group, and *Lyginopteris* is resolved as the sister taxon to all other seed plants considered. The cordaites, *Cordaixylon* and *Mesoxylon*, along with *Lebachia*, extant conifers, and *Ginkgo* constitute a monophyletic group. *Pentoxylon* is the sister taxon to Bennettitales, and the Gnetales are the sister group to angiosperms. Together the Gnetales plus the angiosperms form the sister group to the Bennettitales plus *Pentoxylon*. If the outer integument of bennettitalean and angiosperm ovules is interpreted as homologous with the "cupule" of *Caytonia* and corystosperms, then the corystosperms are resolved as the sister group to the Bennettitales plus *Pentoxylon* plus Gnetales plus angiosperm clade. Under this interpretation all the seed plant taxa considered except *Lyginopteris*, cycads, and medullosans are part of a single clade in which flattened seeds and saccate pollen are primitive. The principal difficulties with the cladistic analysis concern necessary inferences on unknown characters in certain plants, and the current absence of a large base of comparative data. Results of the analysis suggest that the seed ferns as currently circumscribed are not a meaningful group for phylogenetic purposes and permit an evaluation of the possible phylogenetic position of *Eremopteris*, *Nystroemia*, *Spermopteris*, *Phasmatocycas*, Vojnovskiales, *Leptostrobus*, and several other enigmatic groups of plant fossils. Comparison of the phylogenetic analysis with previous theories of angiosperm origin shows that it reconciles the ideas of Arber and Parkin, that Bennettitales and Gnetales are closely related to flowering plants, with more recent hypotheses that invoke *Caytonia* and corystosperms as highly relevant to the angiosperm problem. The results suggest that increased understanding of Triassic Bennettitales, Gnetales, and corystosperms will be of maximum interest in further elucidating the phylogenetic relationships of flowering plants.

The origin of flowering plants is one of the major unsolved problems of plant phylogeny and an enigma in which most major groups of vascular plants have been implicated. Together with the related question of the origin of the angiosperm flower it has generated a body of literature unrivalled in phylogenetic botany for its size and diversity of opinion. The suggestion that *Magnolia* and related taxa are the most primitive living angiosperms (Arber & Parkin, 1907; Bessey, 1897, 1915) originated at around the turn

of the century and reflected a natural extension of the pre-Darwinian systematic tradition of De Candolle and Bentham and Hooker (Davis & Heywood, 1973). The concomitant interpretation of the flower as a reduced bisexual axis bearing ovules and pollen organs on modified leaves (Anthostrobilus or Euanthial theory, Arber & Parkin, 1907) was similarly an extension of the classical idealistic morphology of the nineteenth century. Although the magnoliid theory has never been without its competitors (e.g., Croizat,

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1960; Engler, 1897; Meeuse, 1966; Melville, 1962, 1963; Rendle, 1925, 1930; Sporne, 1971b; Strasburger et al., 1898; Wettstein, 1935), comparative studies of extant flowering plants particularly over the last 20 years (Bailey, 1944; Bailey & Swamy, 1951; Cronquist, 1968, 1981; Dickison, 1975; Eames, 1961; Hickey & Wolfe, 1975; Raven, 1975; Stebbins, 1974; Takhtajan, 1969, 1980; Walker, 1974a, 1974b, 1976; Walker & Doyle, 1975; Wodehouse, 1935, 1936) have reinforced the view that the Magnoliidae sensu lato (Cronquist, 1968, 1981; Takhtajan, 1969, 1980) and perhaps certain monocotyledons (Burger, 1977) are a heterogeneous assemblage of plants that retain a relatively large number of primitive characters for flowering plants as a whole. This conclusion now has been corroborated broadly by the occurrence of the predicted primitive leaf and pollen characters in the earliest angiosperm fossil record (Doyle, 1969, 1973, 1978; Doyle & Hickey, 1976; Hickey & Doyle, 1977; Muller, 1970, 1981, 1984; Sporne, 1974; Upchurch, 1984; Walker & Walker, 1984; Wolfe et al., 1975). The sequential stratigraphic appearance of progressively more complex leaves and pollen (Brenner, 1963; Doyle, 1969; Doyle & Hickey, 1976; Hickey & Doyle, 1977; Hughes, 1976; Muller, 1970, 1984) has been interpreted as documenting a major mid-Cretaceous flowering plant radiation beginning in the Barremian or earlier in the Lower Cretaceous (Brenner, 1984; Trevisan, pers. comm.). Palynological evidence suggests that this radiation began at low, tropical, paleolatitudes and was followed by predominantly poleward migration (Brenner, 1976; Hickey & Doyle, 1977). Reports of pre-Cretaceous angiosperms either have been rejected or must be regarded as of uncertain relevance due to lack of critical information (Doyle, 1978; Hill & Crane, 1982; Scott et al., 1960). Reconstructions of some early angiosperms from several dispersed organs (Dilcher & Crane, 1984) and studies of flowers and other reproductive structures (Basinger & Dilcher, 1984; Crane & Dilcher, 1984; Dilcher, 1979; Krassilov et al., 1983; Vakhrameev & Krassilov, 1979) also have provided important insights into the systematic relationships, floral morphology, and reproductive biology of some early flowering plants.

Despite this success in clarifying the timing and pattern of the early flowering plant radiation, the fundamental question of the phylogenetic position of angiosperms in the overall scheme of seed plant evolution remains unanswered. Some

have claimed that we are no closer to a consensus as to which group of gymnosperms might be most relevant than we were at around the turn of the century (Beck, 1976; Harris, 1960; Hughes, 1976). Discussions of this problem have generally centered on two interrelated issues: the origin of the angiosperm carpel, and the ancestors of flowering plants.

There have been many hypotheses as to the derivation of the angiosperm carpel from the ovulate reproductive structures of living and fossil gymnosperms. The most common proposition derives the conduplicate carpel from the ovulate structures of pteridosperms (seed ferns) sensu lato: either *Caytonia* (Andrews, 1963; Doyle, 1978), corystosperms (Stebbins, 1974), *Glossopteris* (Retallack & Dilcher, 1981), or even Carboniferous seed ferns (Long, 1966, 1977). Although none of these hypotheses has received universal acceptance, they have contributed to a widespread view that the outer integument of the normally bitegmic angiosperm ovule is homologous to the cupule of seed ferns (Smith, 1964), and that the pteridosperms are the ancestors of flowering plants (Cronquist, 1968, 1981; Knoll & Rothwell, 1981; Stewart, 1983).

Much of the literature reviewed above implies that solution of the angiosperm problem must necessarily involve the recognition of angiosperm ancestors (e.g., Mabberley, 1984). This is a position confronted by theoretical and practical difficulties. First, if our current understanding of evolutionary processes is accurate, then it is species, not higher taxa, that are the units of evolution, and thus only species and not higher taxa can be truly ancestral (Eldredge & Cracraft, 1980: 114); and second, ancestral groups cannot be defined by features that they alone possess, because by definition these features also characterize members of the descendant group (Wiley, 1979: 212–214). Under such circumstances it is inevitable that many ancestral groups have been construed loosely and used broadly to indicate inferred proximity of descent. A system in which groups are not clearly defined, and similarity is hazily interpreted as phylogenetic relationship, may have heuristic value, but inevitably it is only capable of generating broad, relatively unspecific conclusions that are difficult to compare. It does not facilitate explicit, and thus critical, evaluation of alternative suggestions of relationship (Hill & Crane, 1982).

Phylogenetic systematics (Hennig, 1966; often treated as synonymous with cladistics) offers an



alternative approach to the question of angiosperm origins. It can provide a relatively explicit assessment of relationships from which straightforward evolutionary interpretations can be made and a methodological framework in which competing theories of relationship may be compared usefully. It also provides an alternative to the search for ancestral groups, allowing phylogenetic problems to be formulated in a different and more tractable fashion. In cladistic terms the problem of angiosperm origin is to recognize and define the major groups of seed plants, to determine their phylogenetic interrelationships, and thus to establish with which group of gymnosperms the flowering plants share a most recent common ancestor (Crane, 1984).

The large-scale phylogenetic relationships of seed plants have been the subject of very little critical discussion, and there is little agreement on how the major taxa should be grouped together. Many recent classifications have either adopted or modified the views of Coulter and Chamberlain (Chamberlain, 1935; Coulter & Chamberlain, 1917) formulated over half a century ago (Bierhorst, 1971; Cronquist et al., 1966; Foster & Gifford, 1974; Sporne, 1971a). Other authors have merely treated all the major groups as of equivalent rank (Bold, 1973; Bremer & Wanntorp, 1981; Taylor, 1981a). The late Professor Tom Harris succinctly summarized the situation when he commented (1976: 133) that the "classes" of gymnosperms were no longer the "branches of a single phylogenetic tree," but "a dozen separate trees rooted in the unknown." This paper attempts to systematize available data on fossil and living seed plants, to clarify their relationships, and establish a coherent framework within which the position of flowering plants may be assessed.

There have been two previous attempts to evaluate relationships within seed plants using cladistic techniques. Both were preliminary and intended in part to stimulate future work. Parenti (1980) produced a highly resolved arrangement of seven major groups, but her analysis was criticized by Smoot et al. (1981) and Young and Richardson (1982) (see also reply by Parenti, 1982). The principal difficulties with her analysis concerned the heterogeneity, and hence monophyly, of some taxa, and the level of detail of character definition. Hill and Crane (1982) presented an analysis based solely on extant seed plants using living *Equisetum*, lycopods, and ferns as out-groups. Our analysis also encountered dif-

ficulties with character definition and recognition. Fifty characters were surveyed but yielded several alternative solutions that, although dramatically different, were almost equally parsimonious. This paper extends and attempts to improve on the analysis by Hill and myself. It reanalyzes and redefines many of the characters employed, includes additional characters, and incorporates for the first time some of the better understood fossil gymnosperms. In the absence of detailed cladistic analyses of the larger gymnosperm groups (e.g., conifers), outline cladograms are proposed as a basis for recognizing advanced and primitive characters in those taxa.

The paper is divided into four major parts. First, the principles of cladistics are introduced briefly and illustrated by a simple analysis of relationships between the three extant genera of Gnetales. Second, the characters of extant, and sufficiently well known fossil, seed plants are reviewed and phylogenetic relationships are assessed. Third, an overview of seed plant phylogeny is presented and compared with previous classifications and phylogenetic hypotheses. Finally, the possible phylogenetic relationships of other more poorly understood plant fossils are reviewed and problems for future research are discussed. Throughout, it should be noted that higher taxa are referred to as far as possible by informal names that have no implication of taxonomic rank. The primary concern is to clarify relationships, and I make no suggestions as to how these should be summarized as a formal nomenclatural scheme. Fossil taxa are treated as "whole plants." Justification for individual cases is given in the text. In the descriptive sections the megasporangiate reproductive structures are referred to as "ovules" except where embryos are known to be present. The terms megasporophyll and microsporophyll are used throughout for simplicity of comparison, but it is by no means clear in many gymnosperms whether the reproductive structures are leaf or shoot homologues. Individual cases are discussed in the text. The numbers assigned to characters are prefixed by the number of the table in which they are listed.

#### PHYLOGENETIC RELATIONSHIPS IN THE GNETALES—A THREE-TAXON PROBLEM

##### PRINCIPLES

In a cladistic analysis each of the taxa under consideration should be a monophyletic group.



As far as I know no one has seriously questioned the naturalness and, by implication, the monophyly of any of the three extant gnetalean genera. *Welwitschia* is in any case monotypic. It is a bizarre xerophyte occurring only in restricted desert areas of southwest Africa (Chamberlain, 1935). *Gnetum* comprises about 40 species of predominantly tropical lianes but also includes a few trees and shrubs (Sporne, 1971a). *Ephedra* comprises about 40 species of "switch" shrubs with less common tree-like and vine-like forms (Sporne, 1971a). The genus occurs in xeric habitats at low, but generally extra-tropical, latitudes.

Not all of the characters of these genera can contribute to resolving relationships within the Gnetales. Features restricted to a single genus may account for its distinctiveness but are clearly of no value for interpreting relationships with other genera. Similarly, features that occur in all three genera may be useful for defining the limits of the Gnetales as a group but cannot contribute to defining inter-generic relationships. Characters that occur in two of the three extant genera may provide an indication of relationship but are of two kinds: those that could define an exclusive group of two gnetalean genera in which no other taxon would be included, and less restricted characters that could only define a group in which non-gnetalean taxa would also have to be included. Characters of the first kind suggest that two gnetalean genera are more closely related to each other than they are to any other taxon, while characters of the second kind merely indicate that the two genera are no more closely related to each other than either is to some non-gnetalean plant. Characters of the second kind are of no value for assessing phylogenetic relationships among the three gnetalean genera, and cladistics attempts to recognize and utilize only characters of the first kind. This is accomplished by assessing the distribution of characters in related groups ("out-group comparison," Hill & Crane, 1982: 280; Stevens, 1980, 1981; Watrous & Wheeler, 1981). Theoretically the out-group for the Gnetales could be all other organisms, but for practical purposes a more manageable out-group could be all other seed plants or all other vascular plants. In this example all seed plants, with the exception of flowering plants, are used as the out-group. The effect of incorporating flowering plants is considered later in this paper.

To assess whether the tetrasporic megagamete-

tophyte of *Welwitschia* and *Gnetum* defines an exclusive group, and therefore suggests close relationship, the distribution of the tetrasporic and monosporic condition is examined in all seed plants. All other seed plants (excluding some angiosperms) are monosporic. The tetrasporic condition is relatively restricted and defines an exclusive group (*Welwitschia* plus *Gnetum*). Conversely, the cellular female gametophyte seen at fertilization in *Welwitschia* and *Ephedra* is merely an expression of the condition that occurs in all other seed plants except *Gnetum* and angiosperms. In *Gnetum* the female gametophyte is partially free nuclear at the time of fertilization. The character is therefore of no value for assessing relationships between the gnetalean genera.

Assessing the generality (polarity) of characters by out-group comparison inevitably involves a logical regress in that decisions can be made only by reference to groups already circumscribed (perhaps wrongly) by the distribution of yet other characters (Hill & Crane, 1982: 280). However, the process can be used to develop a hypothesis about which of a pair of contrasted characters is more, or less, restricted. This is open to test by broadening the analysis still further. When applied to a variety of characters these assessments of generality result in a character hierarchy that defines groups within groups, for example, a multicellular embryo developing within an archegonium (embryophytes), vascular tissue of tracheids and/or vessels (tracheophytes), seeds (seed plants, spermatophytes), or a megaprothallus of four to 16 nuclei (angiosperms) (Fig. 1). In this way relationships can be defined in relative terms (Hennig, 1965: 98). *Ginkgo* and *Pinus* both have seeds (spermatophytes) and are therefore more closely related to each other than either is to *Lycopodium* (a pteridophyte), which is free spor-ing and lacks seeds.

All characters may be useful for defining groups at some level in the hierarchy (Wiley, 1981: 126), but at any given level of inclusiveness (universality) some characters will be useful for group definition, whereas others will not. The implementation of this distinction is the fundamental difference between cladistics and phenetics. At any level in the hierarchy the phenetic concept of "overall similarity" is separated into a generalized, cladistically non-definitional component (symplesiomorphy), and a less generalized, definitional component (synapomorphy).

In practice recognizing apparent synapomor-



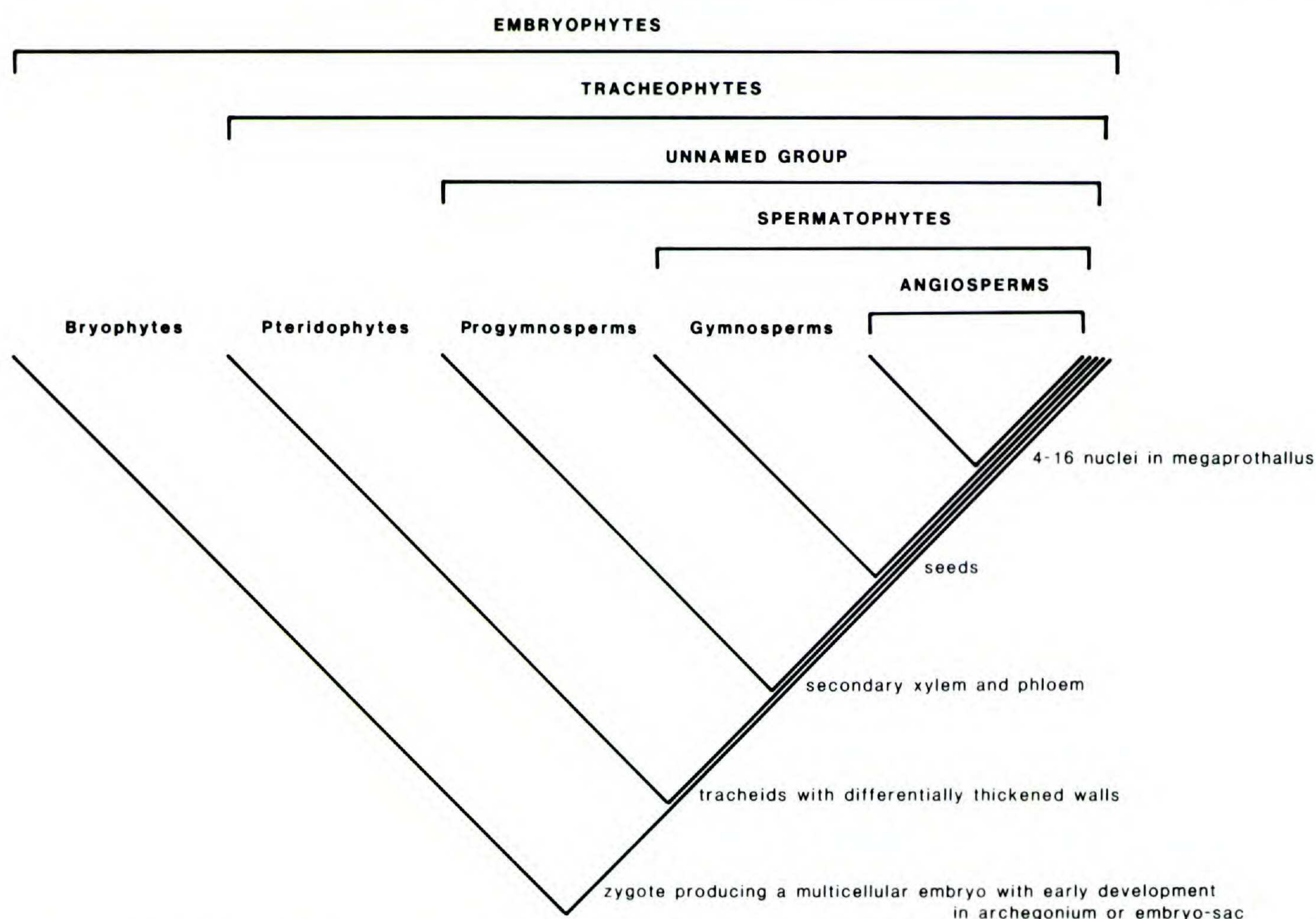


FIGURE 1. A simplified summary of character distributions in embryophytes and the subclasses that they define. Groups definable by presence of a single character given in upper case. Such groups may be regarded as monophyletic. Widely used grade groups only definable by combined presence and absence of characters shown in this diagram are given in lower case. Unless these groups can be shown to have unique defining characters, they are regarded as paraphyletic. For further details of relationships within the bryophyte grade see Mishler and Churchill (1984).

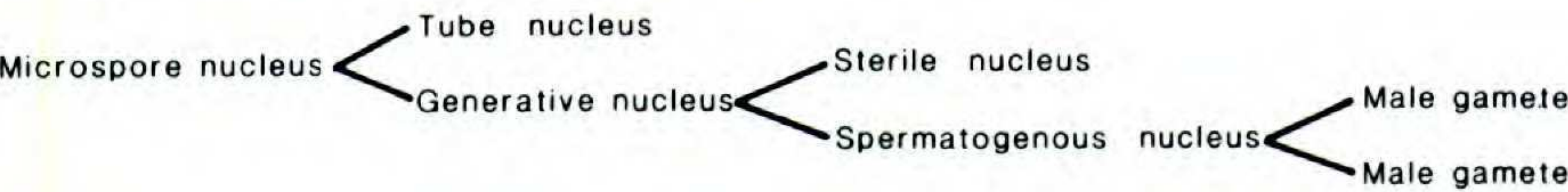
phies and identifying their distribution seldom produces a single unambiguous character hierarchy. Different characters often indicate conflicting groups and hierarchical patterns. Applying the principle of parsimony, it is the simplest of competing patterns that is preferred. In effect, parsimony minimizes the conflict between apparent synapomorphies and therefore the conflict between apparent groups (Farris, 1982; Wiley, 1981). In cladistic terms the "true synapomorphies" recognized in this way are homologies, and the problems of determining polarity, synapomorphy, and homology can therefore be viewed as synonymous (Eldredge & Cracraft, 1980: 35–40; Hill & Crane, 1982: 282–287; Patterson, 1982a; Stevens, 1984). The result of a cladistic analysis is therefore merely a pattern of nested synapomorphies. It defines relationships in a relative way and like any other hierarchical pattern may be summarized in a tree-like diagram. There is no necessary relation to the theory of evolution and no necessary time axis.

Although such diagrams can thus be largely independent of evolutionary preconceptions (Nelson, 1979; Patterson, 1982b; Platnick, 1979, 1982), most systematists wish to interpret them in phylogenetic terms (Crane & Hill, in press; Hill & Crane, 1982; Wiley, 1981). Indeed, for many systematists, the compatibility between cladistic reasoning and current concepts of character change during phylogeny is an important reason for preferring a cladistic rather than a phenetic approach. Interpreted in terms of phylogeny the nested synapomorphies can be viewed as a nested sequence of homologous evolutionary novelties, and the problem of determining character polarity as a problem of deciding which characters represent modifications of which—in other words, which characters are relatively derived or advanced. Groups defined by synapomorphies (clades) can be interpreted as including a common ancestor and all its descendants (monophyletic). Groups such as the gymnosperms and pteridophytes (Fig. 1) that contain

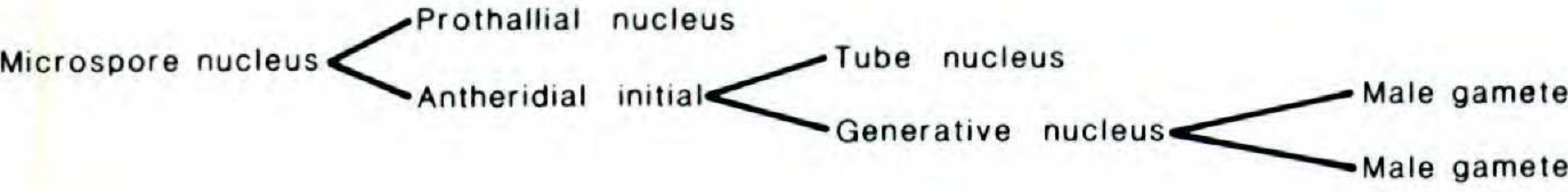


GNETUM, WELWITSCHIA

Sterling (1963)



Martens (1971)



EPHEDRA

Martens (1971)

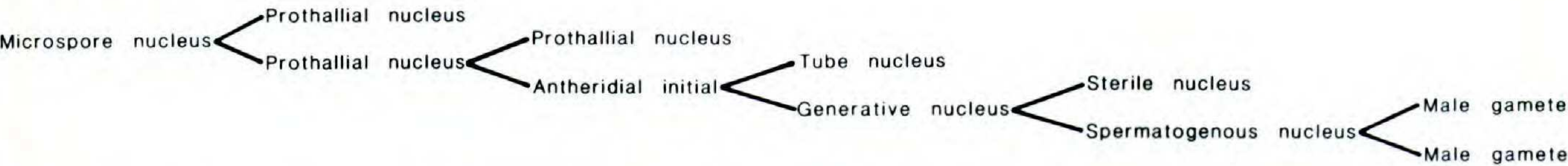


FIGURE 2. Comparison of male gametophyte development in *Gnetum*, *Welwitschia*, and *Ephedra*. See text for further explanation.

some, but not all, of the descendants of a common ancestor (paraphyletic), may be interpreted as definable only by a combination of shared primitive and advanced features. The vertical axis of the cladogram can be interpreted as relative time and the nodes as hypothetical ancestors. Relationships may be viewed in terms of relative recency of common ancestry (Bigelow, 1956; Hennig, 1966). *Ginkgo* shares a more recent common ancestor with *Pinus* than either does with *Lycopodium*. Finally, the principle of parsimony can be viewed as a criterion for selecting between competing cladograms in which homoplasy (parallelism, convergence, and reversal) is minimized.

ANALYSIS OF CHARACTERS

1.1 Male gametophyte composed of four nuclei. In *Gnetum* and *Welwitschia* three haploid mitoses produce a male gametophyte of four nuclei (Martens, 1971; Sterling, 1963), though the pollen may be dispersed at the bi-nucleate or tri-nucleate stage. According to Martens (1971: 146, 260), the gametophyte consists of a prothallial nucleus, a tube nucleus, and a generative nucleus, which produces two male gametes directly without division into sterile and spermatogenous nuclei. Sterling (1963: 195) interpreted the prothallial nucleus of Martens as a “tube nucleus” and the tube nucleus as a “sterile nucleus” (Fig.

2; see Sterling, 1963, for a more detailed consideration of terminology). In *Ephedra*, the microspore undergoes five haploid mitoses to produce a six-celled microgametophyte consisting of two prothallial nuclei, a tube nucleus, a sterile nucleus (stalk nucleus), and a spermatogenous nucleus (body nucleus) (Martens, 1971: 48, 260). The pollen is dispersed with five free nuclei.

The development of the male gametophyte in *Ephedra* is similar to that in *Araucariaceae*, *Pinaceae*, and *Podocarpaceae* (Sterling, 1963). In *Ginkgo* there is also a six-celled microgametophyte, but the details of development (particularly of the motile gametes) differ from those of *Ephedra* and conifers (Lee, 1955). Within the conifers, *Cephalotaxaceae*, *Taxaceae*, *Taxodiaceae*, and most *Cupressaceae* apparently have only three haploid mitoses and lack prothallial cells (Sterling, 1963), as in *Gnetum* and *Welwitschia*. In most cycads, there are four mitotic divisions, and only one prothallial cell is produced (Sterling, 1963). By out-group comparison with pteridophytes I interpret the more extensive five- and six-celled male gametophyte as the more generalized condition and regard the four-celled condition as relatively specialized. Because the conifers are accepted as a monophyletic group in this paper (p. 727), reduction of the male gametophyte must have occurred at least twice in seed plants, once within the conifers, and once within the Gnetales. The character can never-



theless be regarded as a potential synapomorphy in the Gnetales that unites *Gnetum* and *Welwitschia*.

**1.2 Female gametophyte tetrasporic.** In *Gnetum* and *Welwitschia*, the female gametophyte is tetrasporic, being the meiotic product of a single megaspore mother-cell without the formation of cell walls (Martens, 1971: 261). In *Ephedra*, which is monosporic, the megaspore mother-cell produces a linear tetrad of megaspores, the lowermost of which enlarges and divides to form the female gametophyte. Occasionally wall formation between the megaspores may be slightly delayed (Lehmann-Baerts, 1967). The monosporic condition occurs in conifers, *Ginkgo*, cycads, and most angiosperms, and the tetrasporic condition therefore is interpreted on out-group comparison as a derived character.

**1.3 Archegonia absent.** In *Gnetum* and *Welwitschia*, no archegonia differentiate in the female gametophyte (Martens, 1971; Sporne, 1971a). In *Gnetum* this reflects the free nuclear condition of the micropylar end of the gametophyte at fertilization, whereas the female gametophyte of *Welwitschia* is cellular at fertilization, and although archegonial initials can be detected, they do not develop (Singh, 1978). In *Ephedra*, two or three archegonia differentiate from the superficial cells of the gametophyte and consist of an egg cell, a ventral canal cell, and a distinct neck (Martens, 1971, figs. 30, 31). In conifers, *Ginkgo*, and cycads, the archegonia are well differentiated (Sporne, 1971a: 115, 137, 169). From out-group comparison I interpret the absence of archegonia in *Gnetum* and *Welwitschia* as a derived character.

**1.4 Embryo with "feeder."** The mature embryo in *Gnetum* and *Welwitschia* has a lateral, finger-like extension of the hypocotyl, termed a "feeder" (Sporne, 1971a: 179). It remains embedded in the seed after germination and may have an absorptive function. In *Gnetum* the "feeder" is massive and vascularized but is generally less well developed in *Welwitschia* (Martens, 1971: 251). No comparable structure occurs in *Ephedra* or other gymnosperms (Sporne, 1971a: 179), suggesting that it is a specialized feature of *Gnetum* and *Welwitschia*.

**1.5 Ribbed pollen.** Pollen of *Gnetum* is spheroidal, generally 20  $\mu\text{m}$  or less in diameter, with small spinules. The grains are typically inaperturate, but some have a single, thin and poorly defined pore-like area (leptoma) (Erdtman, 1957, 1965: 42–44). Pollen of *Welwitschia* is ellipsoi-

dal, approximately 50  $\mu\text{m}$  long, and the exine has about 20 longitudinal ribs separated by shallow grooves. One of the grooves is larger and forms a poorly defined, elongated aperture (Erdtman, 1957, fig. 30, 1965: 80–81; Wodehouse, 1935, 1936). Pollen of *Ephedra* is similar to that of *Welwitschia*. Grains are ellipsoidal, approximately 20–40  $\mu\text{m}$  long, with 15–18 straight or zig-zag longitudinal ribs separated by grooves that are V-shaped in section. There is no apertural region like that in *Welwitschia* (Erdtman, 1957, fig. 30, 1965: 37–41; Steeves & Barghoorn, 1959; Wodehouse, 1935, 1936). The pollen of living conifers, *Ginkgo*, and cycads shows no close similarities with that of any gnetalean genus; however, the ribbed pollen in *Welwitschia* and *Ephedra* is unique and interpreted here as specialized within seed plants.

**1.6 Vessels.** Vessel elements occur in all three genera of Gnetales. The early protoxylem tracheids are unusual and have circular bordered pits associated with annular or helical wall thickenings (Bierhorst, 1960: 281). These are modified to form pores only in the elements differentiated later in ontogeny (Bierhorst, 1960). In *Gnetum* the later protoxylem tracheids have pores towards their ends. These appear to develop from large pits by loss of pit membranes and frequently by a reduction in the width of the pit border (Bierhorst, 1960: 280–283; Bliss, 1921). Generally there are fewer than six widely spaced pores arranged in a uniseriate row (Bierhorst, 1971: 473). The metaxylem tracheids generally contain fewer pores, and they are arranged in contact with each other. In the secondary xylem, the perforation plates are often transversely oriented and may consist of groups of pores or a single pore (Bierhorst, 1971: 473; Thompson, 1918). These simple plates represent at least two different situations: true simple pores, and compound structures formed by loss of the secondary wall between several adjacent pores (Bierhorst, 1971: 473). Muhammad and Sattler (1982) document the extreme variability in the perforation plates of *Gnetum* and discuss their mode of formation.

In *Welwitschia* the pores in the protoxylem are generally single, and a row of two or three is rare. In the metaxylem and secondary xylem only single pores occur, and there is no evidence that they arise by fusion of several smaller ones as in *Gnetum* (Bierhorst, 1960: 287).

In *Ephedra* the late protoxylem and early metaxylem vessel members typically have more pores than those of *Gnetum*. They are arranged



in a uniseriate row, but in the late metaxylem and secondary xylem the pores tend to be arranged in compact groups. Simple perforation plates are very uncommon (Bierhorst, 1960: 281).

Vessels do not occur in any other gymnosperm and are clearly relatively specialized within seed plants. They are, however, present in some, presumably only distantly related, pteridophytes (Bierhorst, 1958, 1960, 1971). On this basis they are accepted here as a potential synapomorphy of the Gnetales (see p. 767 for discussion of vessels in flowering plants).

*1.7 Microsporangiate and ovulate "flowers" with opposite pairs of bracteoles.* The microsporangiate and ovulate "flowers" of the Gnetales are arranged on a fundamentally similar plan that provides a unifying character for the group. Each "flower" is comprised of a system of opposite and decussate bracteoles axillary to a primary bract (Martens, 1971: 256). Interpretations of the homologies of the bracts, bracteoles, and various envelopes that they form have varied, and an enormous literature has accumulated (Martens, 1971; Pearson, 1929). The explanation of homologies given here is based on a straightforward interpretation of the currently available data.

In *Gnetum* the inflorescences may be "unisexual" or "bisexual," but both are elongated and have whorls of reproductive structures. Microsporangiate and ovulate "flowers" are aggregated into one or more whorls subtended by a fleshy ring-like collar ("cupule" of Pearson, 1929). The base of the inflorescence is subtended by a pair of opposite bracts (Martens, 1971, figs. 102.1, 105.1, 107; Pearson, 1929, fig. 35). The lowermost collar frequently has two teeth oriented at 90° to the two basal bracts, and, if several collars with teeth are present, their arrangement is opposite and decussate (Martens, 1971; Pearson, 1929: 56). Although most collars do not have teeth and show no evidence of bipartite structure in their ontogeny (Martens, 1971: 208–209), they generally are interpreted to have arisen by the phylogenetic fusion of two opposite bracts (Pearson, 1929: 56). In ovulate spikes there are usually one or two rings of fertile ovulate "flowers" (Pearson, 1929: 57–58) above each other. In microsporangiate spikes there are frequently several whorls of "flowers," the upper of which in some species (e.g., *G. gnemon*, Pearson, 1929: 57) are ovulate but "incomplete" (see below) and non-functional. "Floral" primordia develop adaxially from an annular meristem at the base of the su-

praadjacent developing collar (Martens, 1971, fig. 102.4), but the axillary position of the "flowers" is clearly demonstrated by their vasculature. The arrangement of "floral" vascular bundles may be complex, but the traces are predominantly derived from the bundles that supply the collars (Pearson, 1929: 62–68; Thoday, 1911).

The microsporangiate structures of *Gnetum* are surrounded at the base by a tubular "perianth" that has two median lobes at the apex (Martens, 1971: 257; but see Pearson, 1929). There is some indication of bipartite structure during early ontogeny (Martens, 1971: 213, fig. 110.5, 110.6), and the perianth is generally interpreted as having been phylogenetically derived from two posterior-anterior bracteoles (Fig. 3A; Bierhorst, 1971: 475; Sporne, 1971a).

The nucellus in *Gnetum* is surrounded by three envelopes (Fig. 3B) that have been variously interpreted (Martens, 1971; Pearson, 1929). All three layers arise ontogenetically as circular meristems, the outer differentiating first (Martens, 1971, fig. 104). The inner layer, interpreted here as the only integument, is extended at the apex into an elongated micropylar tube that extends beyond the two outer envelopes. The middle and outer layers give no indication of an origin from pairs of opposite bracteoles (Martens, 1971), and that interpretation (Fig. 3C) hinges solely on reconciling the structure of *Gnetum* with that of *Ephedra* and *Welwitschia* (see below). In "incomplete" flowers of *Gnetum* the middle layer begins to develop but then aborts (Chamberlain, 1935: 416).

In *Welwitschia* the microsporangiate and ovulate inflorescences are dichasially branched (Sporne, 1971a: 180), and the ultimate branches terminate in cones with opposite and decussate bracts ("cone-scales," Sporne, 1971a: 180). The microsporangiate "flowers" (Fig. 3D) are the most complex "floral" structures in the Gnetales. Each consists of a central sterile ovule with a single integument and elongated micropylar tube expanded at the apex into a papillose funnel-shaped opening (Martens, 1971: 134–135; Sporne, 1971a). At the base of the ovule there are two small lateral flaps (Martens, 1971, fig. 71.11). The ovule is surrounded by a cup-like structure bearing two lateral, two dorsal, and two ventral microsporangial stalks. Each stalk has a terminal trilocular sporangium that dehisces by three radial slits at the apex. In addition to the two lateral sporangia there are also two lateral "pseudostaminal" primordia (Martens, 1971: 137–142).



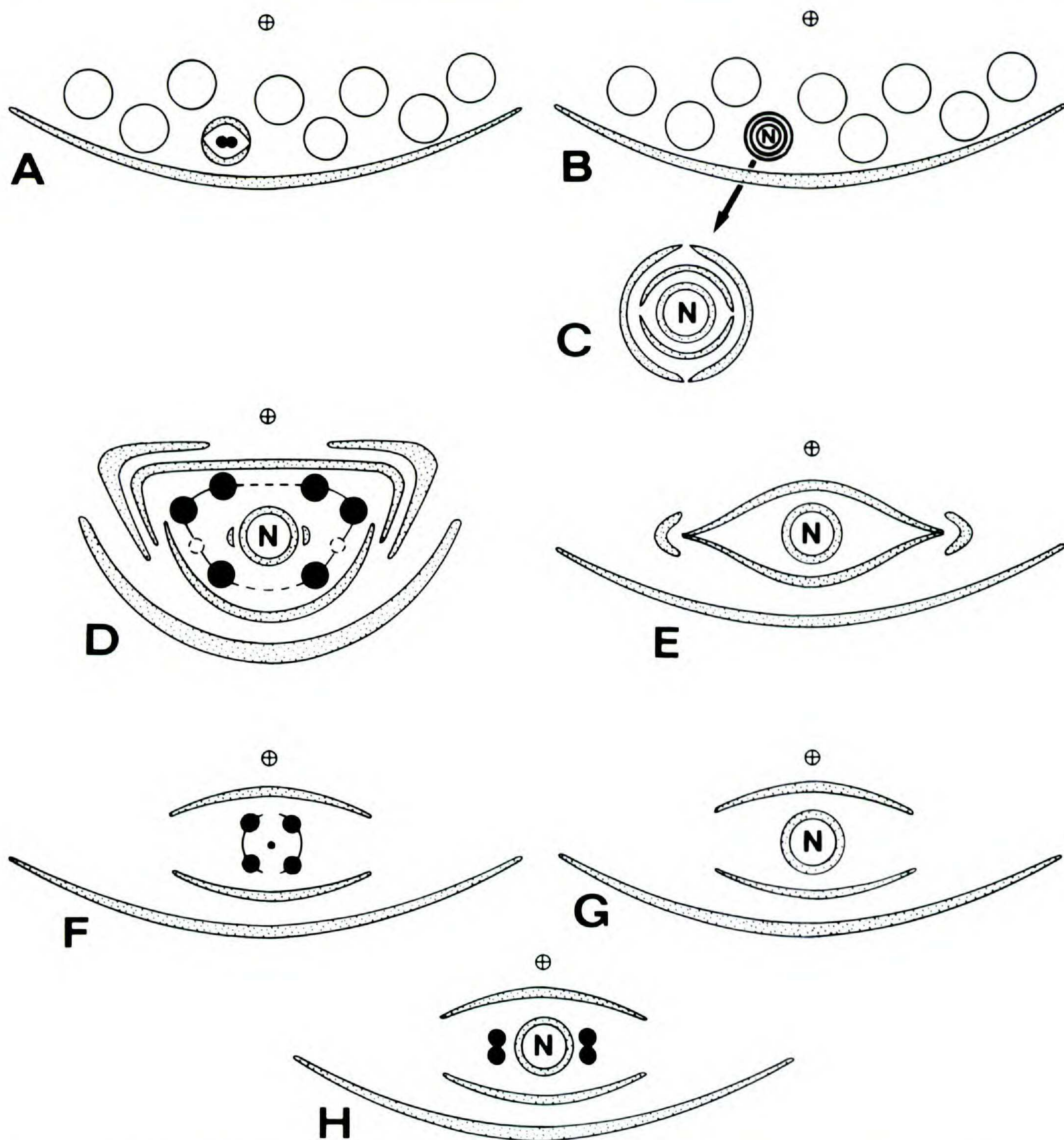


FIGURE 3. Comparison of microsporangiate and ovulate "floral" diagrams in the Gnetales.—A. *Gnetum* microsporangiate "flower," after Martens (1971, figs. 105.4, 105.7, 110.5, 110.6).—B. *Gnetum* ovulate "flower," after Martens (1971, figs. 103, 104).—C. *Gnetum* ovulate "flower," interpretation, see text (character 1.7) for explanation.—D. *Welwitschia* microsporangiate "flower," redrawn from Martens (1971, fig. 70.6).—E. *Welwitschia* ovulate "flower," redrawn from Martens (1971, fig. 63.6).—F. *Ephedra* microsporangiate "flower," after Eames (1952, fig. 1A).—G. *Ephedra* ovulate "flower," based on Martens (1971).—H. *Ephedra* abnormal microsporangiate "flower," after Mehra (1950: 176, pl. V.2). N = nucellus.

Outside the microsporangiate cup there is an inner anterior-posterior pair of bracteoles oriented parallel to the primary bract and an outer pair of lateral bracteoles.

The ovulate "flowers" of *Welwitschia* (Fig. 3E) are organized on a plan very similar to those with microsporangia. The single ovule has an elongated micropylar tube but it is not expanded at

the apex. There are no microsporangiate structures, or any indication of them, but there is an inner pair of anterior-posterior bracteoles (that form the wing in "fruit") and an outer pair of lateral bracteoles.

The microsporangiate and ovulate inflorescences of *Ephedra* are borne in axillary position and vary considerably in their degree of branch-



ing (Pearson, 1929). The “flowers” are clustered into “cones” with an opposite and decussate arrangement of primary bracts. The microsporangiate “flowers” (Fig. 3F) consist of a two-lipped “perianth” that arises from two anterior-posterior primordia (Pearson, 1929: 76) and surrounds the base of the microsporangiate structures. The morphology of the microsporangiate structures varies among species. In *E. distachya*, *E. intermedia*, and *E. trifurca* there are two or more separate sporangiophores, sometimes with a protruding, vascularized axial remnant between them (Bierhorst, 1971: 467; Chamberlain, 1935: 369; Eames, 1952). Eames (1952) interprets this condition as primitive. In other species, such as *E. antisiphilitica* (Bierhorst, 1971: 467), the sporangiophores form a compound columnar tube. Eames (1952) regards this condition as relatively advanced. The number of sporangia varies from two to eight, forming a trilocular, quadrilocular, or more typically bilocular synangium at the apex of the columnar tube (Pearson, 1929: 75).

The ovulate “flowers” of *Ephedra* (Fig. 3G) are organized similarly to those with microsporangia. Generally only the uppermost pair of primary bracts in a “cone” is fertile (Pearson, 1929: 54–55), and the lower bracts frequently become red and fleshy at maturity: presumably they aid in dispersal. Each bract subtends one “flower.” The ovule has a single integument with an elongated micropylar tube that exhibits a range of morphologies in different species (Pearson, 1929: 79). The “perianth” has been variously interpreted (Martens, 1971: 41), but consists of two anterior-posterior bracteoles that may be free or connate at their margins (Eames, 1952: 88). These form the “husk” of the “fruit” at maturity.

There is a direct correspondence between the structure of microsporangiate and ovulate “flowers” in *Ephedra*, and the “perianth” of both appears homologous (Eames, 1952). This is supported further by the similarity of poorly developed “perianths” in ovulate “flowers” to the normal “perianth” in microsporangiate “flowers” (Mehra, 1950: 177–178). There is also a close similarity between the microsporangiate “flowers” of *Ephedra* and *Gnetum* (Pearson, 1929: 75), and the microsporangia in both are supplied by two vascular strands (Mehra, 1950). The arrangement of bracts and bracteoles in these three “flowers” differs from the organization in *Welwitschia* only in the absence of the outer lateral bracteoles from the microsporangiate and

ovulate “flowers.” I suggest that the “perianth” in *Ephedra* and *Gnetum* is homologous with the inner bracteoles of *Welwitschia*, and that merely the lateral outer bracteoles are missing. This suggestion is supported by the fact that the microsporangia in *Ephedra* are in fact arranged in a whorl like those of *Welwitschia*, and that where bisporangiate “flowers” of *Ephedra* have been reported (Mehra, 1950: 168–169) the microsporangia occur where expected (Fig. 3H): surrounding the ovule but inside the “perianth” (Mehra, 1950: 177). Only the two outer envelopes around the ovules in *Gnetum* remain unaccounted for. These show no sign of having fused, either phylogenetically or ontogenetically (but see Martens, 1971: 203), from pairs of bracteoles. However, their position, and the occurrence of microsporangia between the integument and the middle layer (inner bracteoles) in abnormal flowers of *G. scandens* (Thompson, 1916), suggest a direct equivalence with the inner and outer bracteoles of *Welwitschia* (compare Fig. 3C, E). Certainly they cannot be reconciled more easily with the reproductive structures of any other gymnosperm. These views on the homology of gnetalean flowers are summarized in Figure 3; their organization is unique within seed plants. On this basis they are interpreted here as a potential synapomorphy of the Gnetales.

#### DISCUSSION AND INTERPRETATION

The data matrix for the seven characters of the Gnetales is given in Table 1 and the resulting cladogram in Figure 4. The results suggest that the Gnetales are a monophyletic group (see also Arber & Parkin, 1908; Hill & Crane, 1982) within which *Gnetum* and *Welwitschia* are more closely related to each other than either is to *Ephedra*. The Gnetales are separated from all other gymnosperms and united as a group by their fundamentally similar floral organization (character 1.7) and the presence of vessels (character 1.6). Their monophyly is further supported by the occurrence of opposite and decussate leaves in all genera (but not all species, Bierhorst, 1971; Foster & Gifford, 1974; Gifford & Corson, 1971; Sporne, 1971a) and the presence of a stem apex with a discrete tunica (Foster & Gifford, 1974; Martens & Waterkeyn, 1963; Voronin et al., 1973) unlike the typical condition in gymnosperms (Gifford & Corson, 1971; Johnson, 1951; Sporne, 1971a: 110, 133, 167, 184). This agrees with the view expressed by Bierhorst (1971) and Coulter



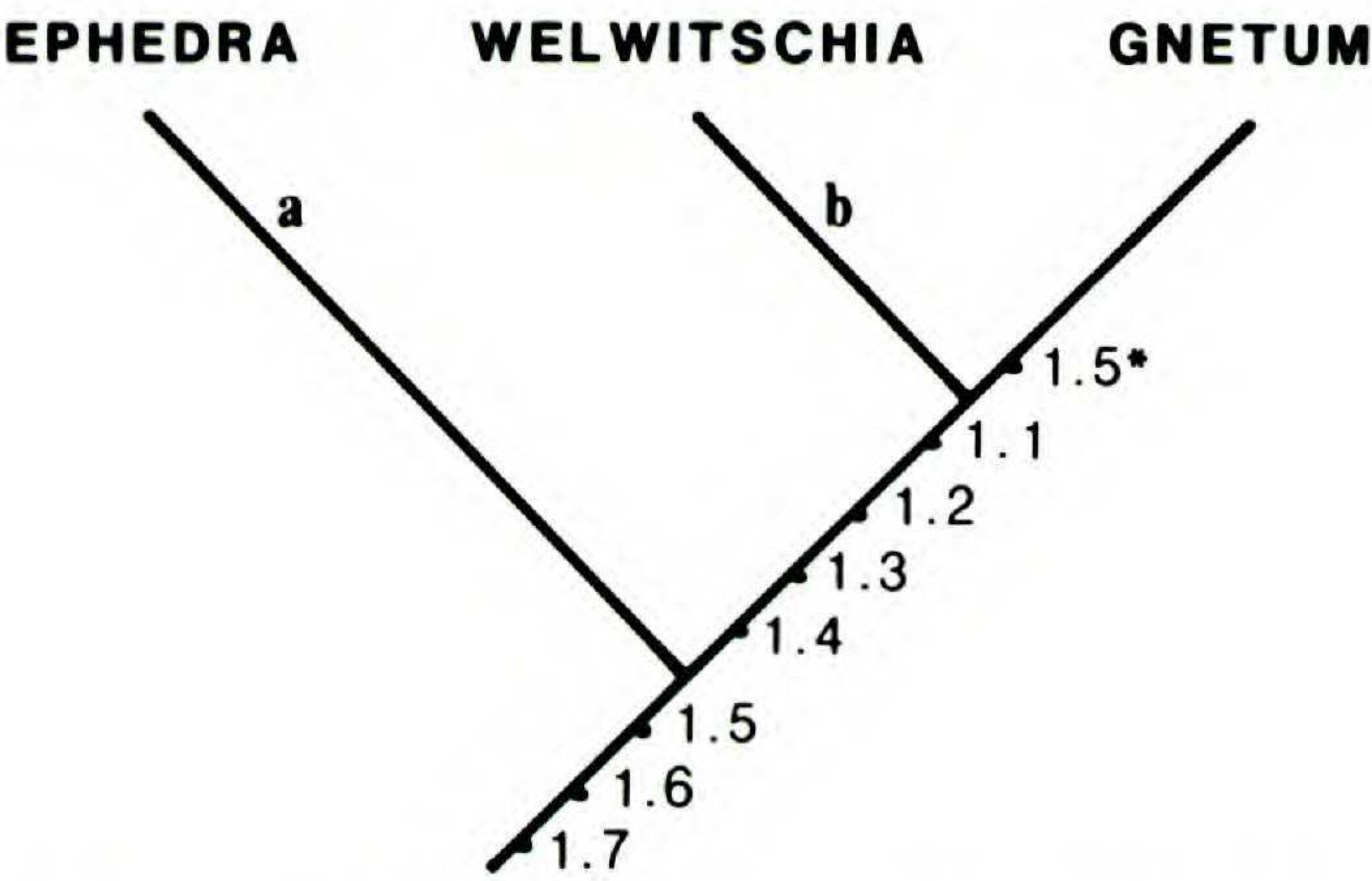


FIGURE 4. Cladogram summarizing relationships between *Gnetum*, *Welwitschia*, and *Ephedra* based on the data in Table 1. See text for further explanation. Viewed methodologically character 1.5 could be interpreted as having been derived independently in *Ephedra* and *Welwitschia* (a, b) or as having been secondarily modified in *Gnetum* (1.5\*). From an evolutionary perspective ribbed pollen is more likely to be primitive within the Gnetales and to have been subsequently modified in *Gnetum*.

and Chamberlain (1917: 402) that, “whatever may be the connections of *Ephedra* with other gymnosperms . . . it cannot be separated from *Welwitschia* and *Gnetum*.”

Additional evidence for a close phylogenetic relationship of *Gnetum* and *Welwitschia* is provided by: the presence of asterosclereids (Bierhorst, 1971: 475; “spicular cells,” Martens, 1971: 255), the occurrence of vestured pits in the early protoxylem (Bierhorst, 1960), the occurrence of paracytic (but not exclusively syndetocheilic) stomata (Florin, 1951, fig. 7e; Maheshwari & Vasil, 1961; Martens, 1971, fig. 96I), totally cellular embryogenesis (Martens, 1971: 765), and the irregular cellularization that occurs during female gametophyte development resulting in multinucleate cells and the formation of fusion

nuclei (Martens, 1971: 262). *Ephedra* is cladistically more primitive. Eames (1952) has emphasized how “distantly related” *Ephedra* is from *Welwitschia* and *Gnetum*, and Coulter and Chamberlain (1917: 403) concluded that, “*Welwitschia* and *Gnetum* are farther removed from other gymnosperms than is *Ephedra*.” Some of the similarities that *Ephedra* shares with conifers have been mentioned above, and in cladistic terms these are interpreted as similarity owing to the retention of plesiomorphic (primitive) characters.

PHYLOGENETIC RELATIONSHIPS  
IN THE CYCADS

Extant cycads comprise ten genera (*Bowenia*, *Ceratozamia*, *Cycas*, *Dioon*, *Encephalartos*, *Lepidozamia*, *Macrozamia*, *Microcycas*, *Stangeria*, *Zamia*) with approximately 100 species in tropical and sub-tropical regions (Greguss, 1968; Sporne, 1971a). They are typically pachycaul, unbranched, with persistent leaf bases, and are generally treated as a natural group (Bierhorst, 1971; Chamberlain, 1935; Sporne, 1971a). A detailed analysis of relationships within cycads is not available, but in this paper I am concerned only with characters that appear to define cycads as a monophyletic group.

ANALYSIS OF CHARACTERS

**2.1 Girdling leaf-traces.** The leaf-traces in cycads arise on the opposite side of the stem to the leaf they supply. They then girdle the stem at a slightly oblique angle before entering the leaf (Chamberlain, 1935: 88–89; Sporne, 1971a: 109). Girdling leaf-traces are not known to occur in any other gymnosperm and are interpreted as a

TABLE 1. Data matrix for characters of the Gnetales.

| Character                                                                    | Other Seed Plants (excluding angiosperms) |                    |               |   |
|------------------------------------------------------------------------------|-------------------------------------------|--------------------|---------------|---|
|                                                                              | <i>Ephedra</i>                            | <i>Welwitschia</i> | <i>Gnetum</i> |   |
| 1.1 Male gametophyte of four nuclei                                          | +/-                                       | -                  | +             | + |
| 1.2 Female gametophyte tetrasporic                                           | -                                         | -                  | +             | + |
| 1.3 Archegonia absent                                                        | -                                         | -                  | +             | + |
| 1.4 Embryo with “feeder”                                                     | -                                         | -                  | +             | + |
| 1.5 Ribbed pollen                                                            | -                                         | +                  | +             | - |
| 1.6 Vessels                                                                  | -                                         | +                  | +             | + |
| 1.7 Microsporangiate and ovulate “flowers” with opposite pairs of bracteoles | -                                         | +                  | +             | + |



**3.1 Narrowly triangular leaves.** The leaf morphology of conifers ranges from narrowly triangular to elongated needles to broad, short scales. In *Agathis* and some species of *Araucaria* and *Podocarpus*, the leaves are broad, leathery, and laminar. Despite this variability, all families, including the Araucariaceae (Stockey, 1982) and



Podocarpaceae (Buchholz & Gray, 1948), have at least some species with narrowly triangular leaves (Bierhorst, 1971, table 25-1; Dallimore & Jackson, 1948). In many conifers ontogenetic evidence is generally interpreted as indicating that helically arranged, narrowly triangular leaves are primitive within the group (Chamberlain, 1935: 358). This is particularly clear in the Cupressaceae, in which the adult foliage frequently consists of opposite and decussate, or whorled, scale-like leaves, but is also seen in other families. The ontogenetic sequence in conifers with well-developed broad, laminar leaves has never been surveyed in detail, but in *Araucaria angustifolia* (*A. brasiliensis*) the early leaves of the seedling are broadly triangular (Hill & DeFraine, 1909). In *Lebachia* the leaves are generally narrowly triangular, occasionally with bifid tips (Florin, 1951; Mapes & Rothwell, 1984; Rothwell, 1982a; Scott & Chaloner, 1983).

I interpret narrowly triangular leaves as the primitive condition in all conifers and regard all other leaf morphologies as secondary modifications of this basic type (but see Discussion and Interpretation). If this view is accepted then leaf morphology distinguishes living conifers and *Lebachia* from other seed plants, which characteristically have large megaphyllous leaves. The closest similarity to the leaves of conifers is found in *Ephedra*, but these are typically arranged in pairs or whorls of three that are joined by a sheathing base around the stem (Foster & Gifford, 1974: 523–524).

**3.2 Resin canals.** Resin canals occur in all conifers, although their distribution in different organs of the plant varies. In some Pinaceae they occur in the cortex of roots and stems, the wood, the leaves, and the ovulate cones. In the Araucariaceae, Cephalotaxaceae, Cupressaceae, Podocarpaceae, and Taxaceae there are typically no resin canals in the secondary xylem (Greguss, 1972) although they usually occur in other parts of the plant, and resin cells are generally present in the xylem parenchyma. Resin canals are particularly sparse in the Taxaceae, especially in *Taxus* (Chamberlain, 1935), but they do occur in the leaves of *Torreya* and the roots of *Austrotaxus* and *Taxus cuspidata* (Chamberlain, 1935: 252). Resin canals occur in Middle Pennsylvanian *Lebachia*-like conifers (Rothwell, 1982a), but lack the epithelial lining seen in many extant conifers.

It is not clear whether the “mucilage canals” of cycads, certain seed ferns, and *Ginkgo* (Bier-

horst, 1971: 375; Sporne, 1971a: 168; Stewart, 1983: 253) are comparable to those of conifers. According to Bierhorst (1971: 375) the contents of these canals in cycads are partly miscible with water and do not appear to have a high terpene content. In this paper I interpret the possession of resin canals as a potential synapomorphy of conifers but closer comparisons, including developmental studies, are needed with secretory structures in other gymnosperms. I interpret the relatively sparse resin canals of *Taxus* as due to secondary loss. There is some limited ontogenetic evidence to support this conclusion. Jeffrey (1903) has reported that in *Sequoia gigantea* resin canals are present only in the secondary xylem of the first year. Resin canals also can be induced by injury in wood that otherwise lacks them (Jeffrey, 1903).

**3.3 Fertile axillary shoot lacking an apical meristem.** It is now widely accepted that the ovulate cones of most conifers are compound structures, the ovuliferous scale being a modified shoot bearing megasporophylls with ovules. Each ovuliferous scale is borne in the axil of a bract. This hypothesis (the polyaxial or “Brachyblast” theory, Florin, 1954) had been proposed by a succession of plant morphologists since the first half of the nineteenth century (see Coulter & Chamberlain, 1917: 245), but was advocated most strongly as a unifying concept by Florin (1951) supported by his observations on Recent and fossil conifers. On this interpretation the most primitive cones would be like those of *Cryptomeria* in which there is little fusion between the ovuliferous scale and the bract and in which the ovuliferous scale has leaf-like lobes. Cones such as those of the Cupressaceae, that show considerable fusion between the bract and ovuliferous scales, are considered relatively advanced. Ontogenetic evidence supports these ideas. In some Taxodiaceae the bract and ovuliferous scales are free when young, but not during subsequent growth (Sporne, 1971a: 141). According to the theory, each ovulate cone is a reduced “inflorescence,” and hence conifers with very poorly developed cones, or with a single bract and ovuliferous scale, as in some species of *Podocarpus*, are regarded as secondarily simplified by reduction (Florin, 1951: 363–367; Wilde, 1944, fig. 40).

According to Florin (1951), only the Taxaceae cannot be accounted for in terms of the polyaxial theory, since the single terminal ovule shows no evidence of having evolved by reduction from a



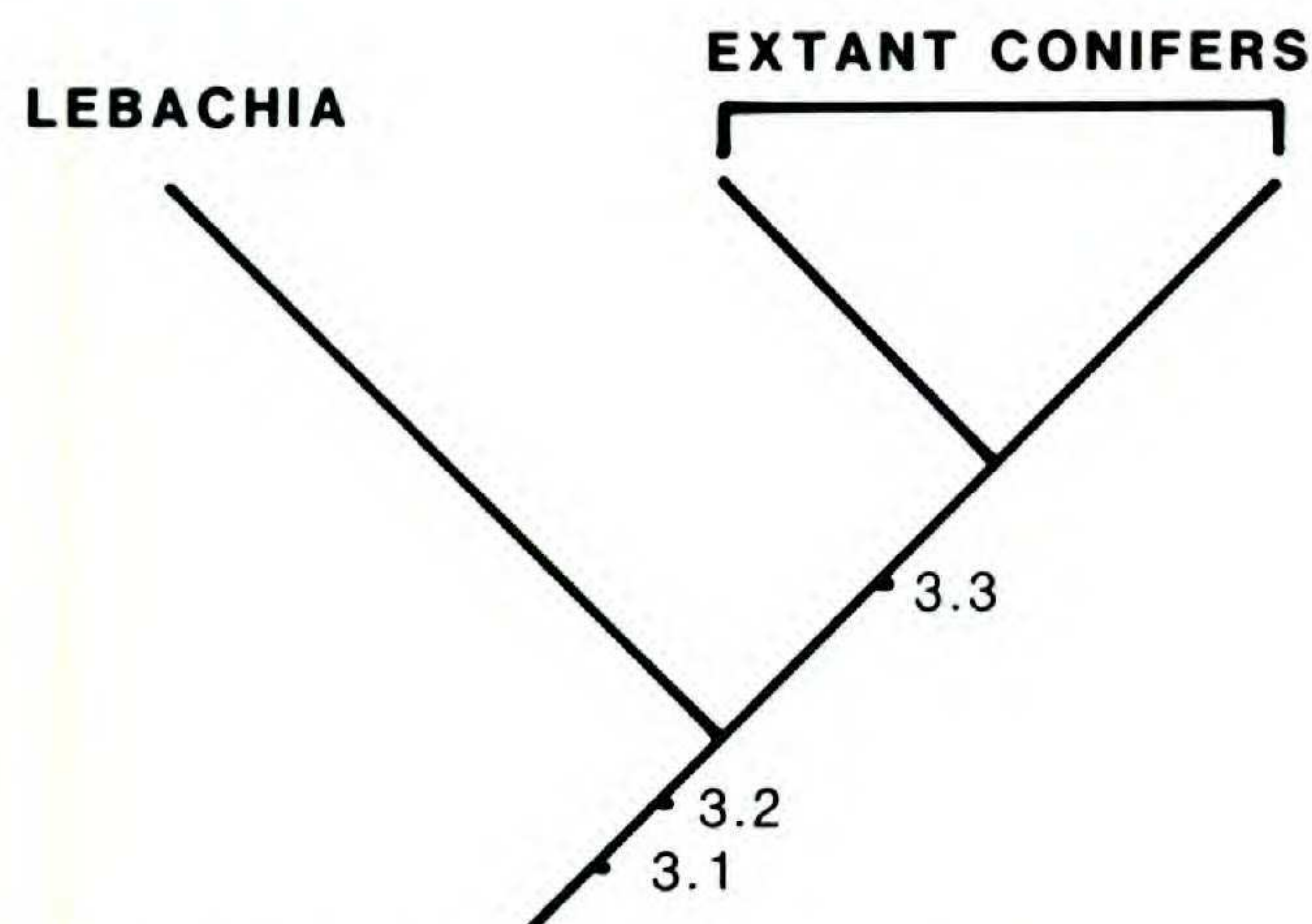


FIGURE 6. Preliminary cladogram summarizing relationships between *Lebachia* and other conifers based on the data in Table 3. See text for further explanation.

bract and ovuliferous shoot system, or from a reduced "inflorescence" (Florin, 1951: 372). Florin (1948, 1951, 1955) regarded this difference from other conifers as fundamental and indicative of a totally independent origin for the two groups. Harris (1976) argued for a closer relationship between conifers and taxads based on a plausible scenario for deriving a terminal taxad ovule from a single fertile axillary shoot. Evidence from stelar morphology is consistent with this view, and "the stelar system of Taxaceae . . . differs in no significant way from the stelar system of conifers with helical phyllotaxy" (Beck et al., 1982: 753).

I treat the Taxaceae as another family within the conifers based on their leaf morphology and the presence of resin canals. Like Harris (1976), I regard the terminal ovule as a secondary simplification from forms with ovuliferous scales (shoots) and bracts. Similar but less extensive simplification is interpreted as having occurred in the Podocarpaceae and Cephalotaxaceae (Florin, 1951; Wilde, 1944). This view is also implicit in those classifications of conifers that regard the Cephalotaxaceae, Podocarpaceae, and Taxaceae as closely related (Buchholz, 1934; Keng, 1975).

Modified fertile shoots in the axils of bracts or leaves also occur in cordaites, *Ginkgo*, and the Gnetales. In cordaites and *Lebachia* the apical meristem of the axillary shoot produces leaves and megasporophylls in a regular phyllotactic spiral (Florin, 1951). However, in all extant conifers the shoot apex is not differentiated (Harris, 1976: 124), and there is no regular phyllotactic spiral. I interpret this as an advance over the condition in *Lebachia* and cordaites, and therefore as a feature that unites all extant conifers.

TABLE 3. Data matrix for characters of conifers.

| Character                                             | Other Seed Plants | <i>Lebachia</i> | Extant conifers |
|-------------------------------------------------------|-------------------|-----------------|-----------------|
| 3.1 Narrowly triangular leaves                        | —                 | +               | +/-             |
| 3.2 Resin canals                                      | +/-               | +               | +               |
| 3.3 Fertile axillary shoot lacking an apical meristem | +/-               | —               | +               |

#### DISCUSSION AND INTERPRETATION

The three characters of conifers considered here are listed in Table 3, and the resulting cladogram in Figure 6. The presence of narrowly triangular leaves and resin canals unites *Lebachia* and extant conifers as a monophyletic group. Rothwell (1982a: 18) has also pointed out that the single plane of symmetry of *Lebachia* seeds is a feature that separates them from those of other platyspermic Paleozoic gymnosperms. This could perhaps be used as a defining character of the group after further study. Within the extant conifer plus *Lebachia* group, the lack of the ovuliferous shoot apex provides a character that defines extant conifers. These conclusions may not be controversial but should be tested by a detailed cladistic analysis of extant, and well-understood fossil, conifers. For example, Beck (1981: 216) raises the intriguing alternative possibility of conifer polyphyly. Based on a consideration of Wilde's work (1944) on Podocarpaceae, he suggests that whereas most conifers may be most closely related to *Lebachia*, the Podocarpaceae may in fact be more closely related to cordaites.

#### PHYLOGENETIC RELATIONSHIPS IN THE GLOSSOPTERIDS



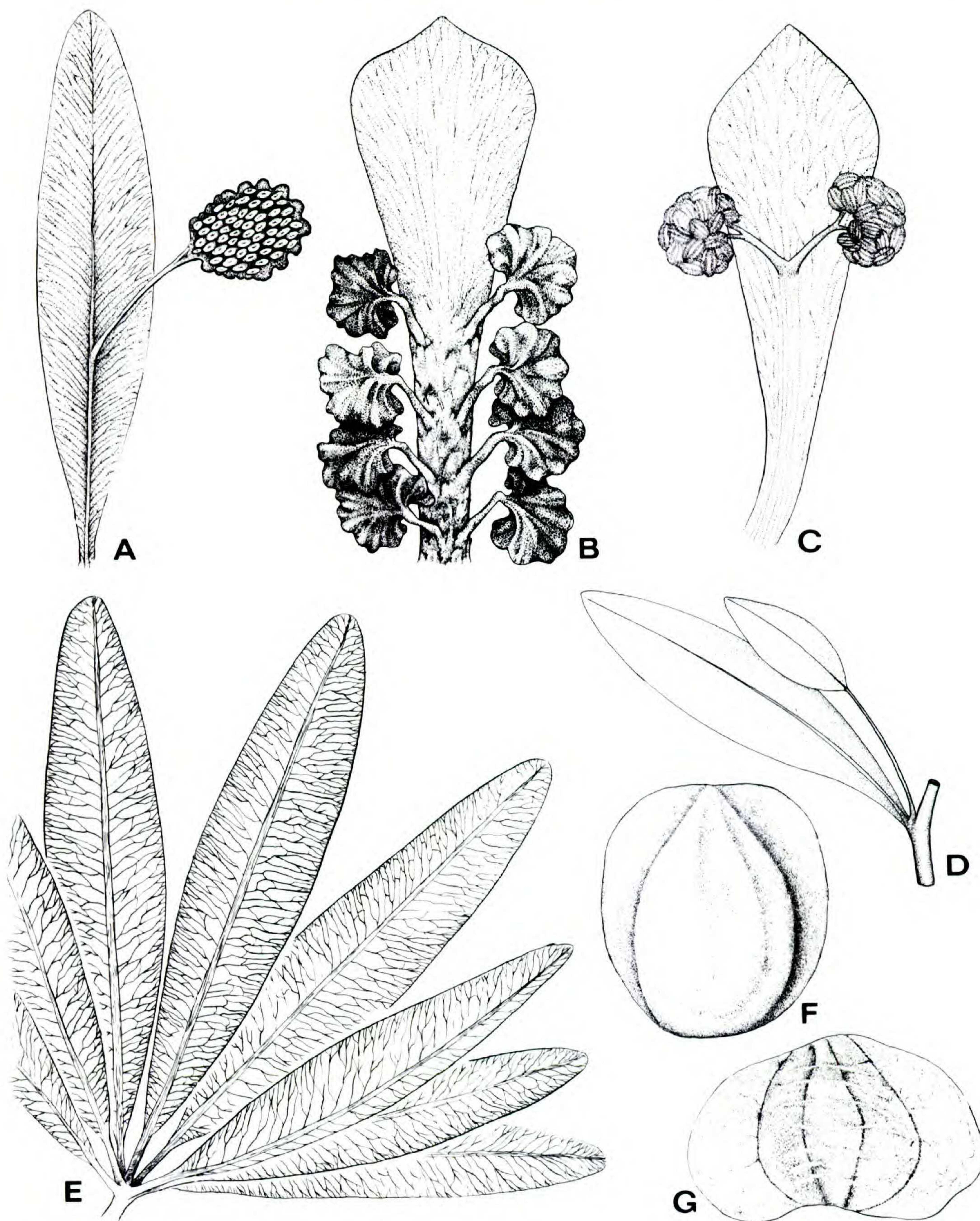


FIGURE 7. Morphology of glossopterids. —A. *Ottokaria* megasporophyll and associated leaf, redrawn from Pant (1977a, fig. 10E–G), orientation of megasporophyll based on Pant and Nautiyal (1984);  $\times 1$ . —B. *Lidgettonia africana* megasporophyll, based on Thomas (1958), Surange and Chandra (1975, text-fig. 12), Schopf (1976, fig. 8D);  $\times 1.5$ . —C. *Eretmonia* microsporophyll, redrawn from Surange and Chandra (1975, text-fig. 1D);  $\times 2$ . —D. “*Glossopteris*” (?*Dictyopteridium*) megasporophyll in axil of a vegetative leaf, redrawn from Gould and Delevoryas (1977, fig. 1d), note that details of sporophyll attachment and sporophyll orientation are uncertain, see text for discussion;  $\times 1$ . —E. *Glossopteris sastrii* leaves borne on a shoot, based on Pant and Singh (1974, text-fig. 2B–D);  $\times 0.5$ . —F. *Pterygospermum raniganjense* platyspermic ovule, based on Pant and Nautiyal (1960, text-fig. 3A);  $\times 25$ . —G. Pollen grain from micropyle of *P. raniganjense*, redrawn from Pant and Nautiyal (1960, text-fig. 4G);  $\times 550$ .



structures have been described (Pant, 1977a; Schopf, 1976; Surange & Chandra, 1975; White, 1978). Unfortunately, many are known only as impressions in which cellular details have not been observed, and their interpretation is therefore equivocal. In this initial analysis I consider only three of the more completely understood glossopterid reproductive structures, "*Glossopteris*" (?*Dictyopteridium*, Gould & Delevoryas, 1977), *Lidgettonia* (Thomas, 1958), and *Ottokaria* (Pant, 1977a; Pant & Nautiyal, 1965).

The ovule bearing structures of most glossopterids were borne adnate to the surface of a leaf. Although they have often been reconstructed adjacent to the adaxial leaf surface (Fig. 7D), this has never been convincingly demonstrated. Glossopterid reproductive structures could be interpreted morphologically in several different ways (e.g., Retallack & Dilcher, 1981, fig. 3), but there are two main possibilities. The ovule bearing structure is either a leaf homologue (megasporephyll) or it is a modified axis (i.e., a cladode). Despite its axillary position, Gould and Delevoryas (1977) emphasized its leaf-like nature, and in this paper I treat it as a megasporephyll. This interpretation also brings the ovulate reproductive structures of glossopterids into line with those of other Mesozoic seed ferns that appear to have megasporephylls.

The anatomically preserved megasporephylls described by Gould and Delevoryas (1977) from the Late Permian of Queensland, Australia were simple, narrowly elliptical with an inrolled lamina, bearing ovules on its inner surface (Fig. 7D). Although Gould and Delevoryas provided some evidence to suggest that the ovule bearing surface faced the subtending leaf, the interpretation remains equivocal and at variance with the reconstruction of *Ottokaria* by Pant and Nautiyal (1984, see below). The gross form of the Queensland material is similar to *Dictyopteridium* described from an impression (Gould & Delevoryas, 1977: 397; Surange & Chandra, 1975). The interior of the structure was filled by a delicate network of filaments, or plates of cells, between the ovules. Based on clusters of *Arberiella* pollen sacs in the Queensland chert, Gould and Delevoryas (1977) suggested that the microsporangiate organs of their plant were of the *Eretmonia* or *Glossotheca* type (Fig. 7C). From other localities *Eretmonia* and *Glossotheca* are known to consist of a fertile portion (interpreted here as a microsporephyll) adnate to a leaf. The microsporephyll consisted of a bifurcated axis, each

branch of which bore numerous *Arberiella* microsporangia. Pollen was bisaccate (*Protohaploxypinus*), with numerous distinct striations on the body of the grain oriented at 90° to the distal suture (Fig. 7G).

*Lidgettonia africana* (Fig. 7B) was described by Thomas (1958) from the Upper Permian of South Africa. It consists of a sterile leaf with an adnate megasporephyll. The megasporephyll differs from that in Gould and Delevoryas' material in bearing about eight fertile "cupules" on slender stalks adnate to the lamina of the subtending leaf. Each "cupule" consisted of an expanded disc, which is thought to have borne ovules on its lower surface. Thomas (1958) interpreted these discs as peltate, but Schopf (1976: 45–48) has shown that the stalk was attached laterally, as in the Indian species *L. mucronata* (Surange & Chandra, 1975). *Arberiella* pollen sacs and microsporephylls of the *Eretmonia* type are associated with the *Lidgettonia* fructifications (Schopf, 1976: 50; Thomas, 1958), but no information is available on the pollen. In this study I assume that it was of the *Protohaploxypinus* type.

*Ottokaria* (Pant, 1977a; Pant & Nautiyal, 1965, 1984) from the Permian of India is preserved as compressions from which some cellular details are known. The megasporephyll was adnate to the upper surface of a leaf and expanded distally to form a "spoon-shaped" head with sterile marginal lobes, bearing ovules on the concave surface (Fig. 7A). Contrary to Gould and Delevoryas' interpretation of the Queensland material, the ovule bearing surface faced away from the subtending leaf (Pant & Nautiyal, 1984). The ovules are similar to the dispersed ovule genera *Pterygospermum* (Fig. 7F) and *Platycardia* (Pant, 1977a; Pant & Nautiyal, 1960). *Protohaploxypinus* pollen ("Striatites," Pant, 1977a) occurs in the micropyles of these dispersed ovules. Apart from the inference that they contained *Protohaploxypinus* pollen, the microsporephylls or microsporangia of *Ottokaria* are unknown. In this paper they are assumed to have been similar to *Eretmonia*.

#### ANALYSIS OF CHARACTERS

**4.1 Glossopterid leaves.** The leaves of all three genera are narrowly elliptical, with reticulate venation. The leaves are distinctive, not known to occur in any other group of gymnosperms, and are interpreted as a specialized char-



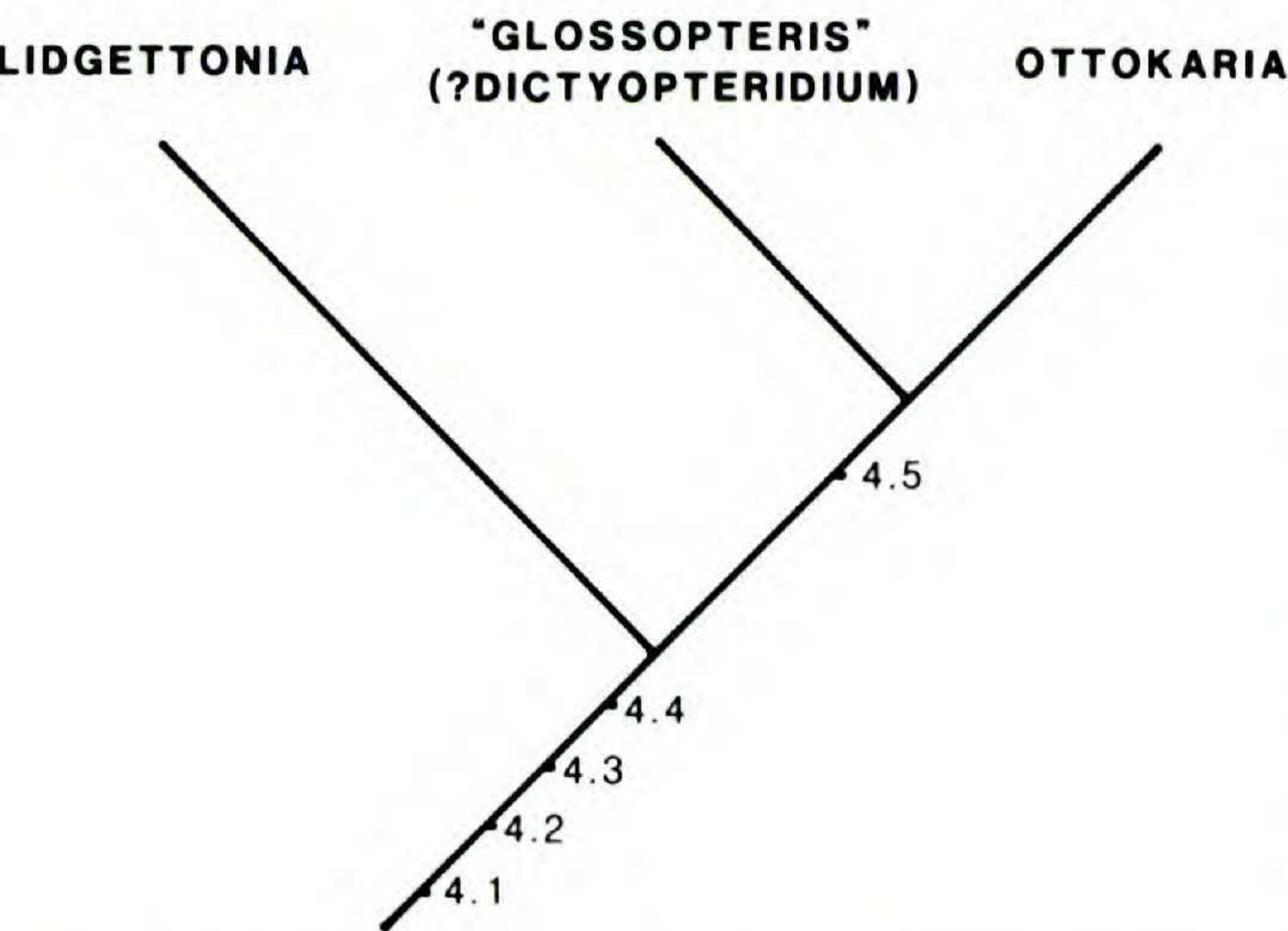


FIGURE 8. Preliminary cladogram summarizing relationships between *Lidgettonia*, “*Glossopteris*” (?*Dictyopteridium*), and *Ottokaria* based on the data in Table 4. See text for further explanation.

acter. The closest similarity in venation occurs in leaflets of *Caytonia* (*Sagenopteris*), but this general pattern of reticulate venation is also widespread in ferns and other groups (Alvin & Chaloner, 1970).

4.2 *Megasporophylls adnate to a subtending leaf.* The megasporophylls in all three genera are adnate or closely adjacent to the subtending leaf. This arrangement is unknown in any other group of seed plants and is interpreted as a specialized character.

4.3 *Microsporophylls adnate to a subtending leaf.* Glossopterid microsporophylls from several localities (Pant, 1977a) are borne adnate to the subtending leaf (Gould & Delevoryas, 1977). This basic arrangement is apparently general in glossopterid plants and is assumed (although not known) to be present in the three glossopterids considered here. It is not known to occur in any other group of seed plants and is interpreted as a potential glossopterid synapomorphy.

4.4 *Striate bisaccate pollen.* Bisaccate pollen with a transverse distal sulcus, and longitudinal striations on the body of the grain, is thought to be general in glossopterids. It occurs rarely in other groups of gymnosperms and some conifers (see also *Nipurdia*, Pant & Basu, 1979). It is interpreted as a specialized character.

4.5 *Simple megasporophyll.* In “*Glossopteris*” (?*Dictyopteridium*) and *Ottokaria*, the ovules are borne on the surface of a simple laminar structure, interpreted here as a simple megasporophyll. Megasporophylls of *Cycas* are similar, but are not adnate to a subtending leaf, and bear ovules only on the margin rather than over the lamina surface. In *Lidgettonia* the presence of several ovule bearing structures suggests that the adnate megasporophyll was pinnate rather than simple as in “*Glossopteris*” (?*Dictyopteridium*) and *Ottokaria*. Pinnate megasporophylls occur in the following seed ferns: *Callistophyton*, peltasperms, corystosperms, and *Caytonia*; and are therefore interpreted here as primitive within the glossopterids. The simple lamina is interpreted, conversely, as a specialized feature that unites “*Glossopteris*” (?*Dictyopteridium*) and *Ottokaria*.

DISCUSSION AND INTERPRETATION

The data matrix for the five characters of glossopterids is given in Table 4 and the resulting cladogram in Figure 8. Glossopterids are defined as monophyletic by four characters (4.1–4.4). Within this group *Ottokaria* and “*Glossopteris*” (?*Dictyopteridium*) are more closely related based on their simple axillary megasporophylls. These conclusions, and the assumptions made, need to be tested by further work. As pointed out by Pant (1977a), there is no evidence to support the suggestion of Surange and Chandra (1975) that the

TABLE 4. Data matrix for characters of glossopterids.

| Character                                        | Other Seed Plants | <i>Lidgettonia</i> | <i>Glossopteris</i> /<br><i>Dictyopteridium</i> | <i>Ottokaria</i> |
|--------------------------------------------------|-------------------|--------------------|-------------------------------------------------|------------------|
| 4.1 Glossopterid leaves                          | —                 | +                  | +                                               | +                |
| 4.2 Megasporophylls adnate to a subtending leaf  | —                 | +                  | +                                               | +                |
| 4.3 Microsporophylls adnate to a subtending leaf | —                 | +                  | +                                               | +                |
| 4.4 Striate bisaccate pollen                     | +/—               | +                  | +                                               | +                |
| 4.5 Simple megasporophyll                        | +/—               | —                  | +                                               | +                |



glossopterids sensu lato should be divided into "pteridospermous" and "glossopterid" forms.

#### PHYLOGENETIC RELATIONSHIPS IN THE BENNETTITALES

The Bennettitales are diverse and abundant plants in Upper Triassic to Upper Cretaceous floras. The leaves may be simple (*Nilssoniopteris*) or, more typically, pinnate, with parallel, occasionally dichotomous veins in the pinnae. In *Dictyozamites* the veins are reticulate. The leaves are superficially like those of cycads but can usually be distinguished by characters of gross form and always by their characteristically cutinized syndetocheilic (paracytic) stomata (Fig. 11C) that contrast with the haplocheilic (anomocytic) stomata of true cycads (Harris, 1932a; Thomas & Bancroft, 1913). Bennettitalean microsporophylls or ovules were aggregated into flower-like heads, usually surrounded by a "perianth" of bracts. The "flowers" were unisexual (monosporangiate) or bisexual (bisporangiate). In all Bennettitales the ovules were orthotropous, with two integuments joined to the nucellus only at the chalaza (see interpretation of *Vardekloeftia* and *Bennetticarpus crossospermus* below; also characters 9.19, 9.22). Distally, the inner integument generally formed an elongated micropylar tube. The ovules were crowded together into heads and individually were not subtended by any other organ. In most compressions of bennettitalean ovules cuticles are obtained from the outer, and usually the inner, surface of the inner integument, the micropylar tube, and the surface of the nucellus; but there is no maceration resistant megaspore membrane (Harris, 1932b, 1954, 1969). The ovules were separated by sterile interseminal scales, which had a single vascular bundle. The morphological nature of these interseminal scales is uncertain, but the structure of *B. crossospermus* described by Harris (1932b) provides evidence to support Seward's view (1913: 118, 1917: 403) that they are homologous with ovules (see also Delevoryas, 1968: 141, interpreted here as bitegmic, p. 764). In *B. crossospermus* (Fig. 9E, F) the elongated micropylar tube passed through the center of a thickly cutinized "micropylar plate" very similar to the flattened cutinized apices of the interseminal scales in the same gynoecium (Fig. 9E). This suggests that the ovules and interseminal scales may be homologous and that the scales "are formed by the diverted development of seed initials"

(Harris, 1932b: 116). Studies of ovule development in *Williamsonia* (Sharma, 1974) also support this idea. There is some evidence that *B. crossospermus* is associated with *Pterophyllum ptilum* leaves (Fig. 9D; Harris, 1932b: 103), but the morphology of the gynoecium is too poorly known to assess the relationships of the plant in more detail. In this paper relationships between 11 of the better understood bennettitalean taxa are considered (Table 5).

*Vardekloeftia* is a genus erected by Harris (1932b) for two species of spherical, bennettitalean, ovulate heads from the Rhaetic of Greenland. Each head was composed of flattened, bilaterally symmetrical ovules separated by numerous interseminal scales. The ovules were relatively few (two to 20), and relatively large (5–7 mm long), compared to those of most Bennettitales. They also were unusual in having an outer cutinized layer (the "cupule," Harris, 1932b, interpreted here as the outer integument) surrounding the inner integument in an identical position to the "micropylar plate" of *B. crossospermus*. Two very similar species have been described, *V. conica*, and the more completely known *V. sulcata*. In *V. sulcata* (Fig. 9B, C), each head contained two to six seeds. In young ovules the cutinized layer outside the inner integument formed a flattened plate through the center of which the micropyle projected. At this stage the outer layer (outer integument) was very similar to the micropylar plate of *B. crossospermus* but was less substantial at maturity. *Vardekloeftia sulcata* is associated with *Pterophyllum kochi* leaves (Fig. 9A; Harris, 1932b: 111), but the microsporangiate structures are unknown.

With the exception of *Vardekloeftia* all other bennettitalean taxa considered in this paper have more ovules in their megasporangiate "flowers" and a well-differentiated "perianth." The basic structure is illustrated by two very similar species, *Williamsonia harrisiana* (Bose, 1968) and *W. sewardiana* (Sahni, 1932b), both based on silicified material from the Upper Jurassic of the Rajmahal Hills, India. These species had a conical or hemispherical receptacle bearing ovules and interseminal scales all over the surface (Fig. 10A). *Williamsonia sewardiana* is thought to have been attached to *Bucklandia indica* stems that bore *Ptilophyllum* cf. *cutchense* leaves (Sahni, 1932b: 10). Both species were apparently unisexual (monosporangiate). Although microsporangiate "flowers" have been described from the Rajmahal Hills (Bose, 1967; Sharma, 1969; Sith-



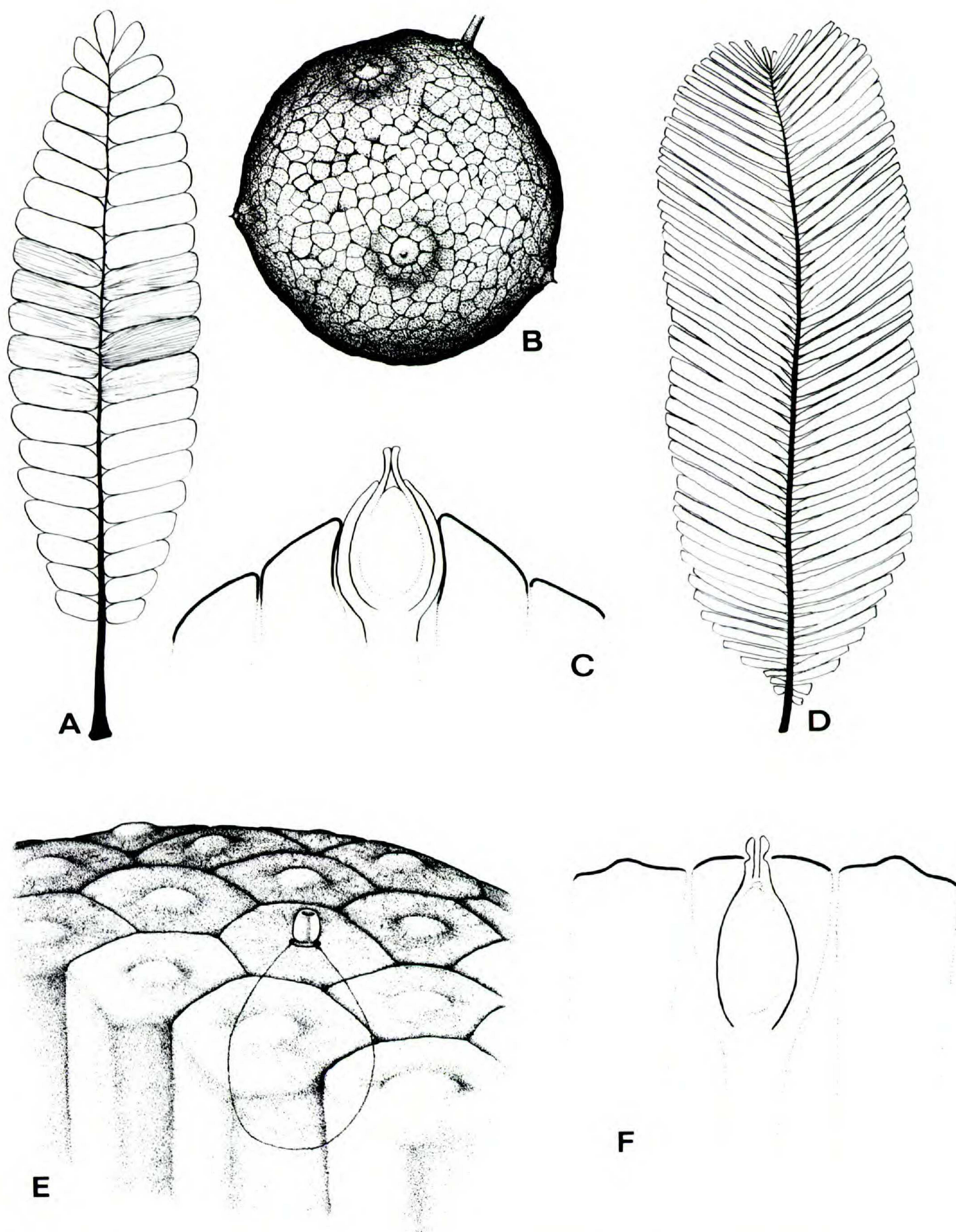


FIGURE 9. Morphology of the *Vardekloeftia* and *Bennetticarpus* plants.—A. *Pterophyllum kochii*, based on Harris (1932b, fig. 29);  $\times 0.5$ .—B. *V. sulcata*, spherical head composed of ovules and interseminar scales, based on Harris (1932b, pl. 15, fig. 1, pl. 17, figs. 1, 2, pl. 18);  $\times 2$ .—C. *Vardekloeftia*, longitudinal section through ovule, redrawn from Harris (1932b, fig. 50E);  $\times 5$ .—D. *Pterophyllum ptilum*, based on Harris (1932b, fig. 30I);  $\times 0.5$ .—E. *B. crossospermus*, outer surface of interseminar scales showing position of ovule, based on Harris (1926, pl. 11; 1932b, fig. 48J);  $\times 10$ .—F. *B. crossospermus*, longitudinal section through ovule, redrawn from Harris (1932b, fig. 50C);  $\times 10$ .



TABLE 5. Isolated organs of the better known Bennettitales.

| Locality                                       | Stem                             | Ovulate Flower                             | Microsporangiate Flower                    | Leaf                                     | Primary Reference |
|------------------------------------------------|----------------------------------|--------------------------------------------|--------------------------------------------|------------------------------------------|-------------------|
| E Greenland (U. Triassic-L. Jurassic)          | ?                                | <i>Vardekloeftia sulcata</i>               | ?                                          | <i>Pterophyllum kochii</i>               | Harris, 1932b     |
| India, Rajmahal Hills (Jurassic)               | <i>Bucklandia indica</i>         | <i>Williamsonia seawardiana</i>            | ?                                          | <i>Ptilophyllum</i> cf. <i>cutchense</i> | Sahni, 1932b      |
| New Mexico (U. Cretaceous)                     | ?                                | <i>Williamsonia harrisiana</i>             | ?                                          | ?                                        | Bose, 1968        |
|                                                | <i>Monanthesia magnifica</i>     | <i>Monanthesia magnifica</i>               | ?                                          | ?                                        | Delevoryas, 1959  |
| Sweden & E Greenland (U. Triassic-L. Jurassic) | <i>Wielandiella angustifolia</i> | <i>Wielandiella angustifolia</i>           | ? <i>Hydropterangium marsilioides</i>      | <i>Anomozamites minor</i>                | Harris, 1932b     |
| U.K., Yorkshire (M. Jurassic)                  | <i>Bucklandia gigas</i>          | <i>Williamsonia gigas</i>                  | <i>Weltrichia sol</i>                      | <i>Zamites gigas</i>                     | Harris, 1969      |
|                                                | <i>Bucklandia pustulosa</i>      | <i>Williamsonia hildae</i>                 | <i>Weltrichia whitbiensis</i>              | <i>Ptilophyllum pectinoides</i>          | Harris, 1969      |
|                                                | cf. <i>Bucklandia pustulosa</i>  | <i>Williamsonia leckenbyi</i>              | <i>Weltrichia pecten</i>                   | <i>Ptilophyllum pecten</i>               | Harris, 1969      |
|                                                | slender (see Harris, 1969: 147)  | <i>Williamsoniella coronata</i> (bisexual) | <i>Williamsoniella coronata</i> (bisexual) | <i>Nilssoniopteris vittata</i>           | Harris, 1969      |
|                                                | ?                                | <i>Williamsoniella lignieri</i> (bisexual) | <i>Williamsoniella lignieri</i> (bisexual) | <i>Nilssoniopteris major</i>             | Harris, 1969      |
| South Dakota (L. Cretaceous)                   | <i>Cycadeoidea</i> sp.           | <i>Cycadeoidea</i> sp. (bisexual)          | <i>Cycadeoidea</i> sp. (bisexual)          | ? <i>Zamites</i>                         | Crepet, 1974      |



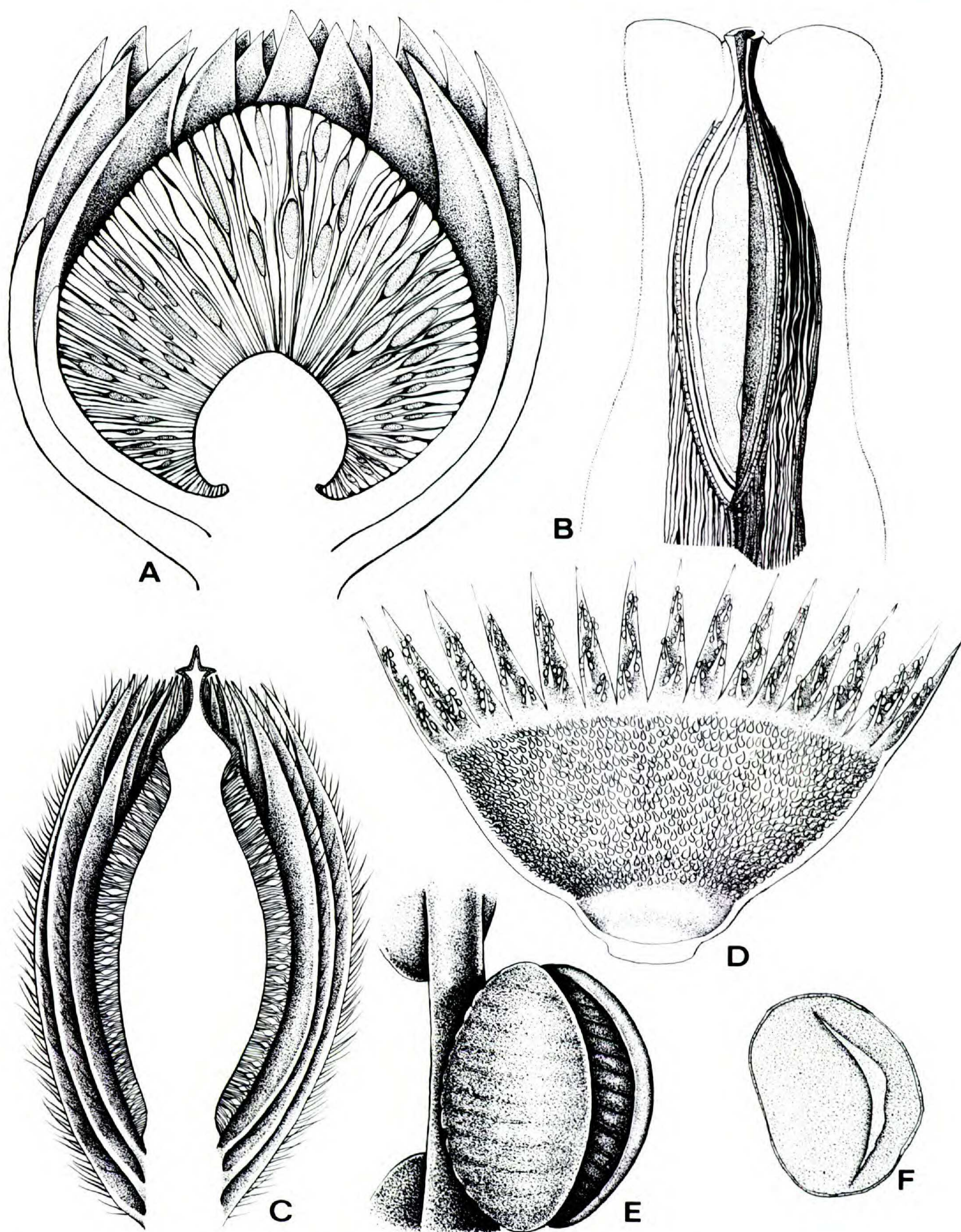


FIGURE 10. Morphology of Bennettitales.—A. *Williamsonia harrisiana*, longitudinal half section of “flower,” based on Bose (1968, pl. 1, figs. 8, 9);  $\times 1.5$ .—B. *Bennettites albianus*, cutaway section through an ovule, based on Stopes (1918, text-figs. 13, 14);  $\times 15$ .—C. *Williamsonia gigas*, longitudinal half section of young “flower,” based on Harris (1969, fig. 56) and Hill et al. (in press);  $\times 1$ .—D. *Weltrichia sol*, longitudinal half section through microsporangiate “flower,” redrawn from Harris (1969, fig. 69E);  $\times 0.5$ .—E. *W. sol*, detail of synangium, based on Harris (1969, fig. 69F);  $\times 10$ .—F. *W. sol* pollen grain, redrawn from Harris (1969, fig. 69A);  $\times 600$ .



oley & Bose, 1953, 1971), the microsporangiate structures of both species, and the vegetative parts of *W. harrisiana*, are unknown.

*Monanthesia* described from the Upper Cretaceous Mesaverde Formation of New Mexico (Delevoryas, 1959) is similar to *Williamsonia sewardiana* and *W. harrisiana*. The “flowers” were monosporangiate and borne on long, slender peduncles in the axil of almost every leaf. The receptacle was conical and covered with ovules and interseminal scales. The microsporangiate “flowers” and pollen are unknown.

Four species of *Williamsonia* have been described based on compressions from the Middle Jurassic of Yorkshire, *W. gigas*, *W. hildae*, *W. leckenbyi*, and *W. himas* (Table 5; Harris, 1969). The first three are the best understood as “whole” plants, and *W. himas* is not considered further in this review. *Williamsonia gigas* (Fig. 10C) has been linked to the leaves *Zamites gigas* and the microsporangiate “flowers” *Weltrichia sol* (Fig. 10D, E; Harris, 1969: 163). *Williamsonia hildae* has been linked with the leaves *Ptilophyllum pectinoides*, the microsporangiate “flowers” *Weltrichia whitbiensis*, the “perianth” bracts *Cycadolepis hypene*, and the stem *Bucklandia pustulosa* (Harris, 1969: 172). *Williamsonia leckenbyi* has been linked to the leaves *Ptilophyllum pecten* and the microsporangiate “flowers” *Weltrichia pecten* (Harris, 1969: 170) (Table 5). The structure of the ovulate “flowers” in all three species is basically similar to that in *Williamsonia harrisiana* and *Williamsonia sewardiana*. The Yorkshire species differ however in the presence of a distinct sterile “corona” above the level at which ovules are borne. The corona is formed from the receptacle and interseminal scales (Fig. 10C; C. R. Hill, pers. comm.; Harris, 1969: 129). The microsporangiate “flowers” of the three plants also are basically similar. *Weltrichia sol* consisted of a whorl of up to 30 “rays” (interpreted here as microsporophylls) more or less fused proximally into a cup-like structure. The inner surface of the cup bore large numbers of “resinous sacs” and the free parts of the microsporophylls bore two-valved synangia (Fig. 10E), each valve of which contained several microsporangia. The pollen was psilate and monosulcate (Fig. 10F). In *Weltrichia sol* (Fig. 10D) there were about 30 microsporophylls, and the synangia were borne alternately on short fertile appendages that projected from the inner surface of the microsporophyll. Comparison with the microsporophylls of *Cycadeoidea* suggests that

these appendages are fertile pinnae. Each valve of the synangium contained about 12–15 microsporangia. In *Weltrichia pecten* and *Weltrichia whitbiensis* there were between ten and 20 microsporophylls, each with sessile synangia in two rows on their inner surface.

*Wielandiella angustifolia* from the Rhaetic of Scania, southern Sweden (Nathorst, 1909), and Greenland (Harris, 1932b) had monosporangiate “flowers” (Harris, 1932b: 90–91). The ovulate “flowers” are similar to those of *Williamsonia gigas*, *Williamsonia leckenbyi*, and *Williamsonia hildae* and have a distal sterile corona. The microsporangiate flowers are poorly understood and require restudy (Lundblad, 1950: 73), but the “palisade rings” described at the base of the “flower” by Nathorst (1909) are similar to *Hydropterangium marsilioides* (Lundblad, 1950). The leaves of *Wielandiella angustifolia* are thought to be *Anomozamites minor*.

Two similar species of *Williamsoniella* are known as compressions from the Middle Jurassic of Yorkshire (Harris, 1944, 1969, 1974). Both were bisporangiate (bisexual) “flowers” (Fig. 11A, D). A whorl of bracts formed a “perianth” around a whorl of about 12 laterally compressed, wedge-shaped microsporophylls. Each microsporophyll bore two or three pairs of short fertile appendages on the adaxial surface (interpreted as fertile pinnae), each of which bore a single two-valved synangium containing pollen sacs with psilate monosulcate pollen. At the center of the “flower” the receptacle bore ovules and interseminal scales and was expanded distally into a terminal sterile corona. The two species, *Williamsoniella lignieri* and *Williamsoniella coronata* (Fig. 11D), are linked with *Nilssoniopteris major* and *N. vittata* (Fig. 11B, C), respectively (Harris, 1969: 146, 149). *Williamsoniella lignieri* was larger than *W. coronata* and generally is less well understood. “Perianth” bracts are associated with the “flower” but have not been seen attached.

Many species of *Cycadeoidea* have been described from a wide range of Upper Jurassic and Lower Cretaceous localities in the Northern Hemisphere (Crepet, 1974; Stewart, 1983; Wieland, 1906, 1916), but all show a basically similar structure. *Cycadeoidea* was pachycaul, with short, stout trunks and helically arranged leaf bases that probably bore *Zamites*-like leaves (Seward, 1917; Wieland, 1906: 87). The “flowers” were bisporangiate (bisexual) (Fig. 11E) and borne on short pedicels in leaf axils. They did not project beyond the persistent leaf bases. There was a perianth of



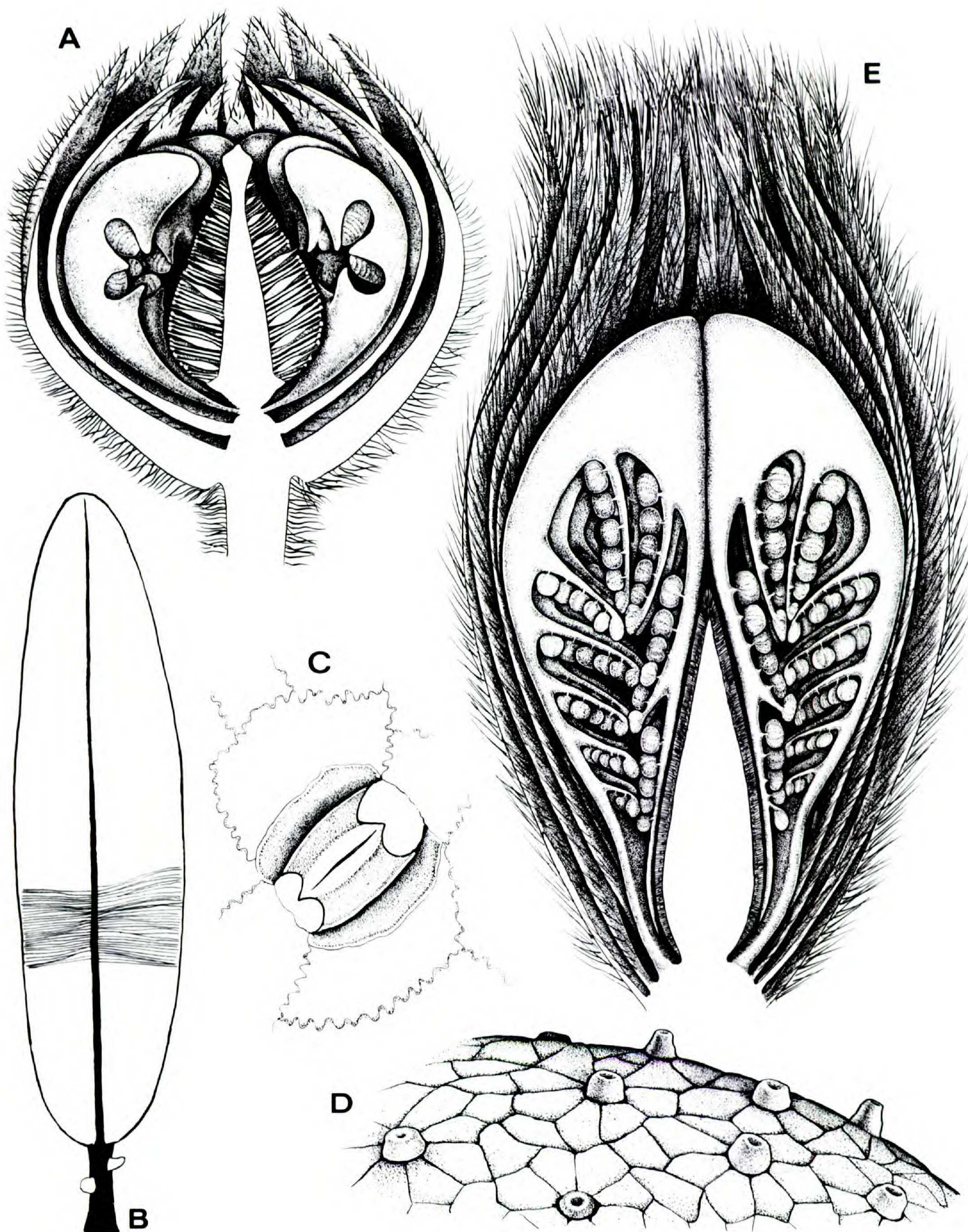


FIGURE 11. Morphology of Bennettitales.—A. *Williamsoniella coronata*, longitudinal half section through “flower,” based on Harris (1944, fig. 1);  $\times 3$ .—B. *Nilssoniopteris vittata*, redrawn from Harris (1969, fig. 32A), an unusual specimen showing two lateral pinnae at the base;  $\times 1$ .—C. *N. vittata*, detail of stoma showing paracytic guard cells and sinuous anticlinal flanges, based on Harris (1969, fig. 32D);  $\times 1,000$ .—D. *W. coronata*, surface of immature “gynoeceium” showing micropyles and interseminal scales, based on Harris (1969, fig. 62F);  $\times 50$ .—E. *Cycadeoidea* sp., longitudinal half section through “flower,” based on Wieland (1906, fig. 88) and Crepet (1974, pl. 61, fig. 21);  $\times 1.5$ .



helically arranged outer bracts surrounding approximately 20 microsporophylls. These were fused proximally into a shallow cup but were pinnate distally and compressed laterally. Two rows of appendages (pinnae) were borne adaxially, each with a row of about six kidney-shaped synangia. The synangia contained eight to 20 tubular sporangia and produced psilate, monosulcate, granular-walled pollen (Crepet & Zavada, pers. comm.). Towards their apices the microsporophylls were incurved, with their abaxial surface against a conical or domed receptacle covered with ovules and interseminal scales, and showing no sign of a corona. Delevoryas (1963, 1968) and Crepet (1972, 1974) both support the view that the microsporophylls never opened to become fully expanded as Wieland (1906) supposed.

#### ANALYSIS OF CHARACTERS

**6.1 Interseminal scales.** Interseminal scales occur in all Bennettitales considered in this analysis. They are not known to occur in any other seed plant, and following Harris (1932b) I interpret them as developing from ovule primordia (see characters 9.19, 9.22). They are regarded here as a specialized character.

**6.2 Guard-cells, paracytic and heavily cutinized.** The stomata of all Bennettitales are paracytic and interpreted as ontogenetically syndetocheilic (Harris, 1932a; Thomas & Bancroft, 1913). This is sufficient to distinguish them from the stomata of most other gymnosperms except *Gnetum*, *Welwitschia*, and some conifers (Scott & Chaloner, 1983). However, the guard-cells of the Bennettitales also have characteristic, heavily cutinized, outer periclinal walls and dorsal anticlinal flanges. This feature occurs in leaves with both sunken and superficial stomata but is not thought to occur in other gymnosperms (Harris, 1932a: 94–108).

**6.3 Ovulate heads with numerous ovules.** All of the Bennettitales considered in this study have numerous (more than 100) ovules in their megasporangiate heads. In *Vardekloeftia*, although only two to six seeds develop per head, there are a large number of interseminal scales that are interpreted as sterile ovule primordia. No other gymnosperms (except the Vojnovskyaceae and Ruflorinaceae, Meyen, 1984) have such a large number of ovules clustered together, and I interpret this as a potential synapomorphy of the Bennettitales.

**6.4 Bivalved synangia.** Most bennettitalean microsporophylls have the microsporangia within bivalved synangia. Although the microsporangia of *Vardekloeftia*, *Williamsonia seawardiana*, *W. harrisiana*, and *Monanthesia* are unknown, the bivalved condition is interpreted here as general in the Bennettitales. In many seed plants (e.g., conifers, cycads) the microsporangia are not in synangia; where they do occur (e.g., *Caytonanthus*, medullosans, and Gnetales), they are not arranged to form a bivalved capsule. Here I interpret the bivalved synangia of Bennettitales as a specialized condition, although it should be noted that they do not occur in all bennettitalean pollen organs (e.g., *Leguminanthus siliquosus* Kräusel & Schaarschmidt, 1966).

**6.5 "Perianth" of helically arranged bracts.** All of the Bennettitales considered in this study, with the exception of *Vardekloeftia* (Harris, 1932b), have ovulate heads that are surrounded by a "perianth" of numerous helically arranged bracts. This flower-like arrangement does not occur in any other group of gymnosperms and is thus interpreted as a relatively specialized feature within the Bennettitales.

**6.6 "Corona."** A "corona" occurs in *Williamsonia gigas*, *W. hildae*, *W. leckenbyi*, *Wielandiella angustifolia*, and the two species of *Williamsoniella*, *W. coronata* and *W. lignieri*. No comparable feature occurs in other gymnosperms, and I regard this as a specialization over the condition in other Bennettitales.

**6.7 Bisporangiate (bisexual) "flowers."** Bisporangiate "flowers" occur in *Cycadeoidea* and the two species of *Williamsoniella*. They are not known in other gymnosperms except the Gnetales (see character 1.7). They are interpreted here as a specialized feature within the Bennettitales, and the possibility that they are homologous with the "flowers" of the Gnetales is considered later in this paper (p. 775).

**6.8 Microsporophylls laterally flattened.** In those Bennettitales for which the microsporophylls are known, only in *Cycadeoidea*, *Williamsoniella coronata*, and *W. lignieri* are they laterally flattened. Dorsiventrally flattened leaf-like microsporophylls are generalized in seed plants, and the laterally compressed forms found in some Bennettitales are therefore interpreted as specialized.

**6.9 Microsporophylls with three to four pairs of bivalved synangia.** Both species of *Williamsoniella* have very similar microsporophylls, with three to four pairs of bivalved synangia. Other



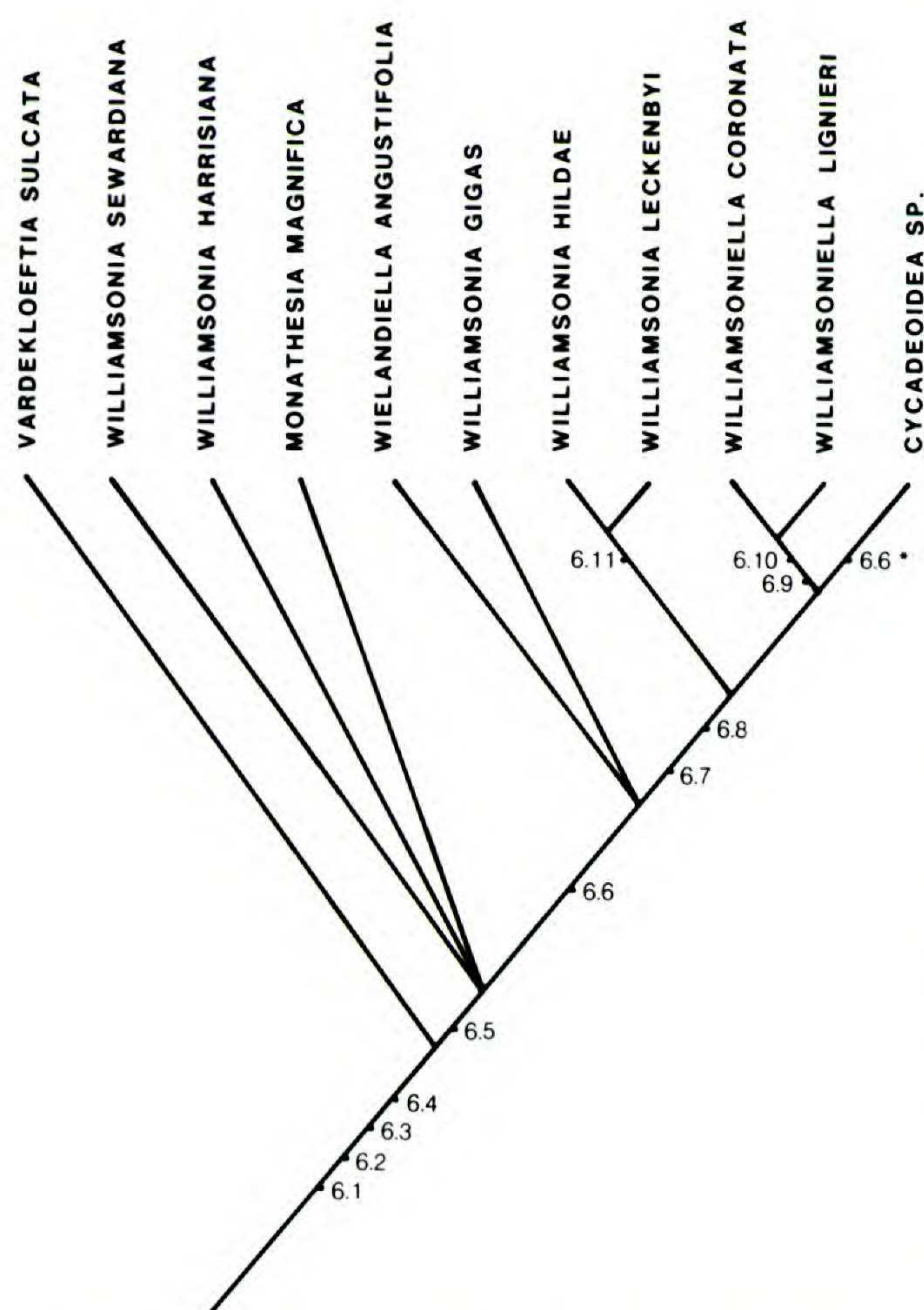


FIGURE 12. Preliminary cladogram summarizing relationships within the Bennettitales based on the data in Table 6. An asterisk indicates reversal of character 6.6. See text for further explanation.

gymnosperms generally have larger numbers of sporangia on each microsporophyll, and most other known bennettitalean microsporophylls have numerous synangia. The condition with few synangia is interpreted as a synapomorphy of *Williamsoniella* species.

**6.10 *Nilssoniopteris* leaves.** Both species of *Williamsoniella* have been linked with *Nilssoniopteris* leaves, and although recognized as two distinct species, *N. vittata* and *N. major* are very similar in morphology, venation, and cuticle (Harris, 1969: 75). Megaphyllous leaves in most seed plants, including most Bennettitales, are pinnate. In the context of the Bennettitales as a whole I therefore interpret *Nilssoniopteris* leaves as a synapomorphy of *Williamsoniella* species.

**6.11 Synangia borne directly on the "rays" (microsporophylls).** The microsporangiate "flowers" of *Williamsonia hildae* (*Weltrichia whitbiensis*) and *Williamsonia leckenbyi* (*Weltrichia pecten*) are extremely similar (Harris, 1969: 169), and differ from the microsporangiate flowers of *Williamsonia gigas* (*Weltrichia sol*) in having the synangia borne directly on the sur-

face of the "rays" (microsporophylls) rather than on fertile lateral pinnae as in *Weltrichia whitbiensis*, *W. pecten*, *Williamsoniella*, and *Cycadeoidea*. The presence of these distinct fertile lateral pinnae is interpreted here as a primitive feature within the Bennettitales based on comparison with the pinnately divided microsporophylls of most "seed ferns."

#### DISCUSSION AND INTERPRETATION

The data matrix for the Bennettitales is given in Table 6 and the resulting cladogram in Figure 12. The Bennettitales have long been widely accepted as a natural group and at this level of analysis may be defined as monophyletic by the presence of interseminal scales, the characteristic cutinization of the guard-cells, the numerous ovules, and the bivalved synangia. The preliminary analysis presented here is the first attempt to clarify the interrelationships of the various taxa within the group. Although it provides some resolution, it is handicapped by lack of knowledge of microsporangiate organs in *Vardekloeftia*, *Williamsonia seawardiana*, *W. harrisiana*, *Wielandiella angustifolia*, and *Monanthesia*. In addition there is considerable diversity among Upper Triassic bennettitalean reproductive structures that needs to be incorporated into the analysis (Kräusel, 1948, 1949; Kräusel & Schaarschmidt, 1966). Several of these fossils (e.g., *Haitingeria krasseri*, *Leguminathus siliquosus*, *Leuthardtia ovalis*, *Westerheimia pramelreuthensis*) have unusual morphologies compared to the "flowers" of later Bennettitales and are currently being reinvestigated (Crane, work in progress).

It has been traditional to recognize two loosely defined families, the Cycadeoidaceae and Williamsoniaceae, within the Bennettitales (Stewart, 1983; Taylor, 1981a), but these do not form monophyletic groups in the cladogram. The Cycadeoidaceae are generally regarded as unified by having the flowers borne within an armor of persistent leaf bases and would include *Cycadeoidea* and *Monanthesia* considered in this analysis. The habit of these plants is similar but other characters do not place them together, and the flowers of *Williamsonia seawardiana* also are surrounded by at least some persistent leaf bases (Sahni, 1932b; see also Sharma, 1971). Unless other characters can be found to unite the Cycadeoidaceae, the two traditional families of Bennettitales have dubious phylogenetic utility. It should, however, be noted that the pattern of characters







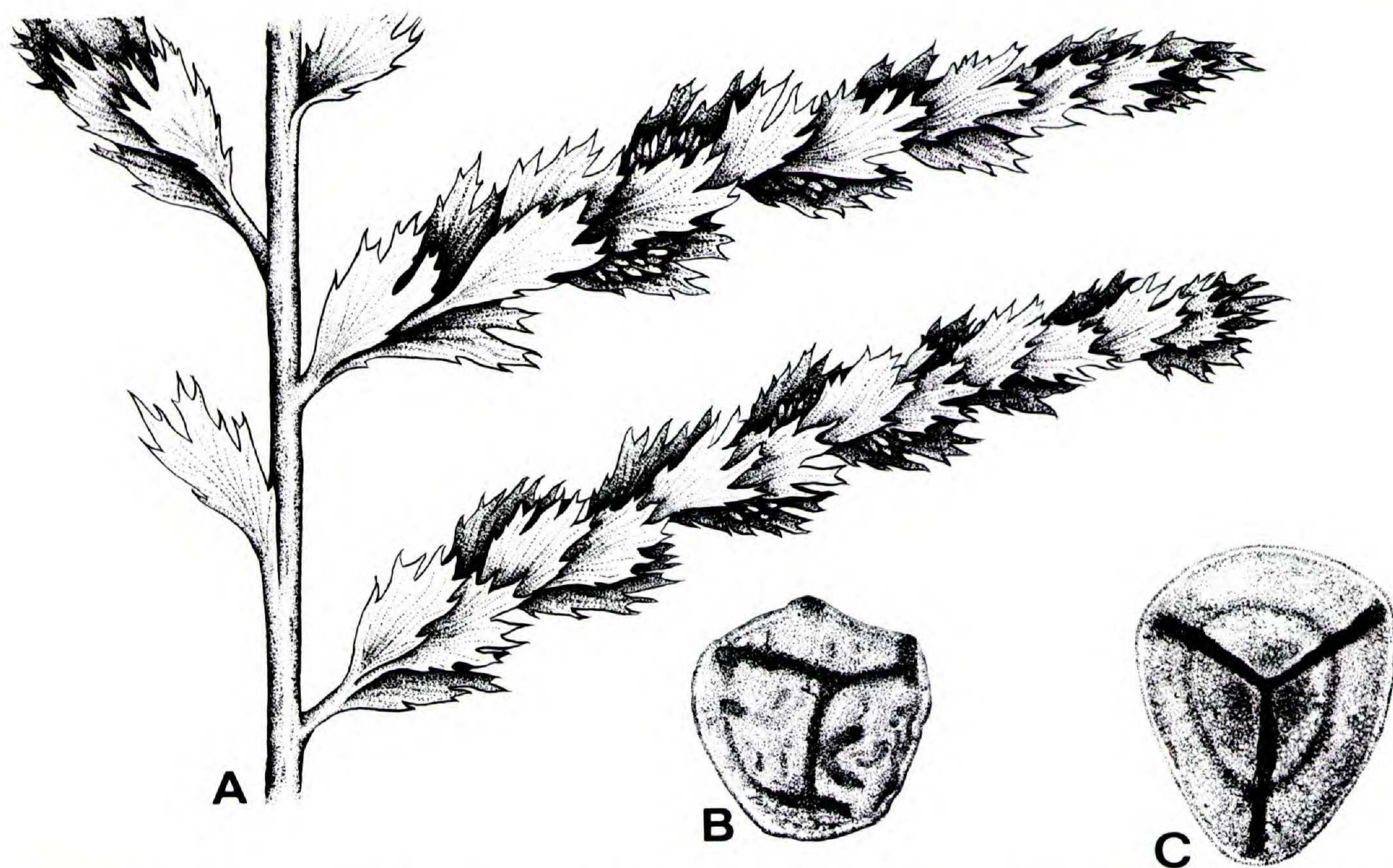


FIGURE 13. Morphology of *Archaeopteris*.—A. *A. macilenta*, fertile lateral branch systems based on Beck (1981, fig. 6.31) and Phillips et al. (1972, pl. 37, fig. 8); ca.  $\times 1.5$ .—B. *Archaeopteris* sp. trilete microspore, based on Phillips et al. (1972, pl. 45, fig. 49);  $\times 500$ .—C. *Archaeopteris* sp. trilete megaspore, based on Phillips et al. (1972, pl. 43, fig. 28);  $\times 200$ .

accepted here suggests that the absence of the "corona" (character 6.6) from *Cycadeoidea* may be interpreted as secondary loss.

#### REPRESENTATIVE EXTANT AND FOSSIL GYMNOSPERMS

Having attempted to provide an outline of relationships within some groups of gymnosperms, the relationships between major seed plant taxa can be assessed. The principal constraint in such an analysis is the information available for many fossil seed plants. In this analysis I have attempted to keep assumptions concerning unknown characters to a minimum by using only the better understood fossil seed plants. This has excluded many potentially important fossil plants that need to be incorporated in future, more inclusive analyses. In this section I briefly review the characters of extant and fossil seed plants, emphasizing in particular the basis and limitations of our knowledge of fossil taxa.

#### ARCHAEOPTERIS

*Archaeopteris* (Fig. 13A) ranges from the mid-Devonian (Givetian) to Lower Mississippian (Tournaisian). It is an important Late Devonian

plant and is the most completely understood of all progymnosperms (Beck, 1981; see Fig. 1). The plants were arborescent and eustelic with a large parenchymatous pith. There was a bifacial cambium that produced both secondary xylem and secondary phloem (Beck et al., 1982). The secondary xylem (*Callixylon*) was pycnoxylic and similar to that of extant conifers. The tracheids had uniseriate to multiseriate, circular, bordered pits on the radial walls (Beck, 1981: 202), and there was no axial parenchyma. The rays were uniseriate to multiseriate. *Callixylon* wood is known to have been attached to *Archaeopteris* branch systems (Beck, 1960, 1970). Although stem morphology and the pseudomonopodial branching of *Archaeopteris* is well understood, regular axillary branching does not occur (Beck, 1981: 212; Scheckler, 1978). Leaves were helically or decussately arranged and decurrent at the base (Fig. 13A), typically wedge-shaped, and varied from entire to deeply divided. The stomata of *Archaeopteris* have not been described.

Some lateral branch systems were fertile. The fertile leaves were generally deeply divided and bore microsporangia and/or megasporangia on their adaxial surface. Some species were heterosporous (Phillips et al., 1972), but whether other



species were homosporous or heterosporous is unknown. The microsporangia were long and slender, while megasporangia were shorter and broader. Both dehisced by a single longitudinal suture. The microspores (*Cyclogranisporites*) were about 40  $\mu\text{m}$  in diameter, with a proximal trilete suture and a finely granular or smooth surface (Fig. 13B). The exine structure was granular (Pettitt, 1966). The megaspores (*Biharisporites*) were about 200  $\mu\text{m}$  in diameter, with a trilete suture and a reticulate to rugulate surface (Fig. 13C; Phillips et al., 1972). Both microspores and megaspores presumably germinated proximally to produce free-living male gametophytes with motile spermatozooids and female gametophytes with well-developed archegonia. However, nothing is known of gametophyte development, gametes, or embryogenesis.

#### MEDULLOSANS

The medullosans are among the most extensively studied of all seed ferns (Stewart, 1983; Stidd, 1981a, 1981b). Typically, they have two or more vascular segments in the stem but this apparent "polystely" appears to be only a modification of the fundamentally eustelic arrangement in all other seed plants (Basinger et al., 1974; Beck et al., 1982). However, *Quaestora amplexa* (Mapes & Rothwell, 1980) from the Upper Mississippian of Arkansas, the earliest medullosan stem known, has an exarch proto-stele. If *Quaestora* is correctly interpreted as a medullosan it suggests that "polystely" may have arisen within the medullosan clade. The bifacial cambium produces secondary xylem and secondary phloem. The wood has multiseriate rays and is comprised of tracheids with multiseriate, oval, bordered pits on their radial walls. Despite extensive studies of medullosan anatomy (Stewart, 1983) and ontogeny (Delevoryas, 1955), axillary branching in medullosans has been demonstrated only once (Hamer, 1984 and pers. comm.). Medullosan leaves (e.g., *Alethopteris*, *Neuropteris*, *Odontopteris*) were large and pinnately organized, often with a bifurcated primary rachis. The petioles (*Myeloxylon*) contained a large number of scattered vascular bundles. Stomata have been described as paracytic (Oestry-Stidd & Stidd, 1976), but reinterpretation and better preserved material shows that they are anomocytic (Mickle & Rothwell, 1982; Reihman & Schabillion, 1978; Stidd, 1981a: 67).

Although a few specimens are known that show

seeds apparently attached to medullosan foliage (Stewart, 1983: 260–261), most medullosan seeds, particularly those that are well understood anatomically (e.g., *Pachytesta illinoensis*), are linked with the vegetative parts on the basis of association evidence (Stewart, 1983: 260). The ovules (*Pachytesta*, *Trigonocarpus*, etc., see Hoskins & Cross, 1946; Taylor, 1965) are large (up to 11 cm long) and radiospermic. Each has a single integument with a sarcotesta, sclerotesta, and endotesta. The integument and nucellus are free except at the chalaza. Frequently the sclerotesta has three primary ribs, and often secondary and tertiary ribs also are developed. The ovules have a radially arranged double vascular system. The outer system has numerous traces that run within the sarcotesta between the ribs, while the inner system within the nucellus is formed by bundles or a network originating from a pad of vascular tissue at the chalazal end. The megaspore membrane in medullosan seeds is thick (5–25  $\mu\text{m}$ ) (Taylor, 1965).

Some medullosan pollen organs are large, complex synangiate structures with tubular sporangia that dehisce longitudinally (e.g., *Dolerotherca*), while others such as *Aulacotheca* and *Halletheca* are simpler, with fewer sporangia (Taylor, 1981b). Only a few of these pollen organs are known to have been attached to medullosan foliage (Dennis & Eggert, 1978), but convincing association and structural evidence has been presented for others (Ramanujam et al., 1974; Stewart, 1983). The majority of the pollen organs are known to have produced *Monoletes* (*Schopfipollenites*) pollen. These grains are large (100–500  $\mu\text{m}$  long) and ellipsoidal. Distally there are often two longitudinal grooves and proximally a monolete suture with a marked deflection in the center. Occasionally (*Parasporites*, Dennis & Eggert, 1978) the grains have a pair of small sacchi. The pollen wall is alveolar, with numerous fine cavities (Taylor, 1978). Pollen wall ultrastructure is similar to that of cycads, but the ontogeny is apparently different (Taylor, 1982; Taylor & Rothwell, 1982), and the wall cavities are much less regular. Germination is thought to have been proximal (prepollen sensu Chaloner, 1970a); male gametes were probably motile. *Monoletes* pollen has been described in the pollen chamber of *Pachytesta hexangulata* (Stewart, 1951). Little is known of male gametophyte development, but the pollen contents figured by Stewart (1951) are suggestive of the spermatozooids of extant cycads and hence zooidogamy.



The details of female gametophyte development are unknown in medullosans, but the gametophyte is cellular, with archegonia at fertilization (Stewart, 1951). Nothing is known of embryogenesis, and an embryo has never been described from a medullosan seed (Stewart, 1983: 282–283).

#### CYCADS

Possible defining characters of cycads have already been discussed (Fig. 5). The primary vascular architecture of extant cycads is not understood clearly (Beck et al., 1982), but evidence from microsporangiate cones suggests that the vasculature is fundamentally eustelic (Beck et al., 1982: 755). Typically the stem has a large pith, and the bifacial cambium (or cambia in *Encephalartos* and *Macrozamia*, Sporne, 1971a: 108) produces relatively small amounts of secondary xylem and phloem. The secondary xylem consists of tracheids with multiseriate bordered pits and has many rays. In *Zamia* and *Stangeria* the wood has tracheids with scalariform pitting (Sporne, 1971a: 108). The growth of most cycad stems is sympodial (see character 2.2), and some genera (e.g., *Stangeria* and *Bowenia*) are irregularly branched. According to Bierhorst (1971: 373), Stopes (1910), and Stevenson (1980) branching is adventitious, and Foster and Gifford (1974: 419) observed that some lateral buds form from the living tissues of persistent leaf bases while others arise due to injury. There are no detailed developmental studies of branching in cycads. Cycad leaves are generally large and pinnate with dichotomous venation, although some anastomoses do occur (Foster & Gifford, 1974: 422–423). The stomata are anomocytic.

The ovules are borne on simple megasporophylls that are generally arranged in cones (see character 2.2). There are generally two ovules per megasporophyll, although some species of *Cycas* may have up to eight. The ovules are large (up to 6 cm long, Chamberlain, 1935: 104) and radially symmetrical. Each has a single massive integument with three layers: a fleshy sarcotesta, a hard sclerotesta, and an endotesta. The integument and nucellus are “fused” except close to the micropyle. The ovule is supplied by a double, radially arranged, vascular system. There are about ten vascular bundles that run up the outside of the sclerotesta, and an inner anastomosing system of vascular bundles that run in the endotesta to the level at which the integument

and nucellus are free. The megaspore membrane is well developed and may be up to 10  $\mu\text{m}$  thick in mature ovules (Chamberlain, 1935: 126; Erdtman, 1965), but the nucellus and inner lining of the integument is only weakly cutinized (Harris, 1954).

The microsporophylls of all cycads are borne in cones and bear microsporangia on their abaxial surface. In *Cycas* there may be more than 1,000 microsporangia, but in *Zamia* there are 25 or less (Chamberlain, 1935: 115). The microsporangia are arranged in sorus-like clusters of two to six, each supplied by a single vein (Stevenson, 1982). Each microsporangium dehisces by a single slit towards the center of the “sorus.” The pollen is boat-shaped, non-saccate, and more or less smooth-walled. The pollen wall is alveolate with numerous fine cavities (Audran & Masure, 1977). The male gametophyte is generally five-celled (see character 1.1), and the final division of the spermatogenous cell produces two large spermatozoids up to 400  $\mu\text{m}$  in length (Norstog, 1977) with a spiral band of flagella (Sporne, 1971a: 116). The pollen germinates distally, producing a haustorial pollen tube, and the spermatozoids are released by a rupture in the pollen tube close to the distal pollen wall.

The female gametophyte develops from a single functional megaspore (see character 1.2) that undergoes free nuclear divisions until over 1,000 nuclei have been produced, before centripetal cellularization (Sporne, 1971a: 114) and the formation of archegonia. Following fertilization, free nuclear division produces 64–1,000 nuclei before cellularization occurs (Sporne, 1971a: 116).

#### LYGINOPTERIS

*Lyginopteris oldhamia* is known from the Upper Carboniferous (Westphalian A) of Europe (Oliver & Scott, 1904; Stewart, 1983). The name is applied to small stems, up to 4 cm in diameter (Taylor & Millay, 1981: 38), of possibly vine-like habit (Stewart, 1983; Taylor & Millay, 1981). The primary vasculature was eustelic (Beck et al., 1982; Scott, 1923), and a bifacial cambium produced relatively little secondary xylem and phloem. The wood contained large tracheids with multiseriate, oval bordered pits on the radial walls. The rays were wide and multiseriate. Regular axillary branching occurred. Leaves were widely separated and borne helically on the stem. They were small, pinnately organized, and highly dissected. The primary rachis bifurcated shortly



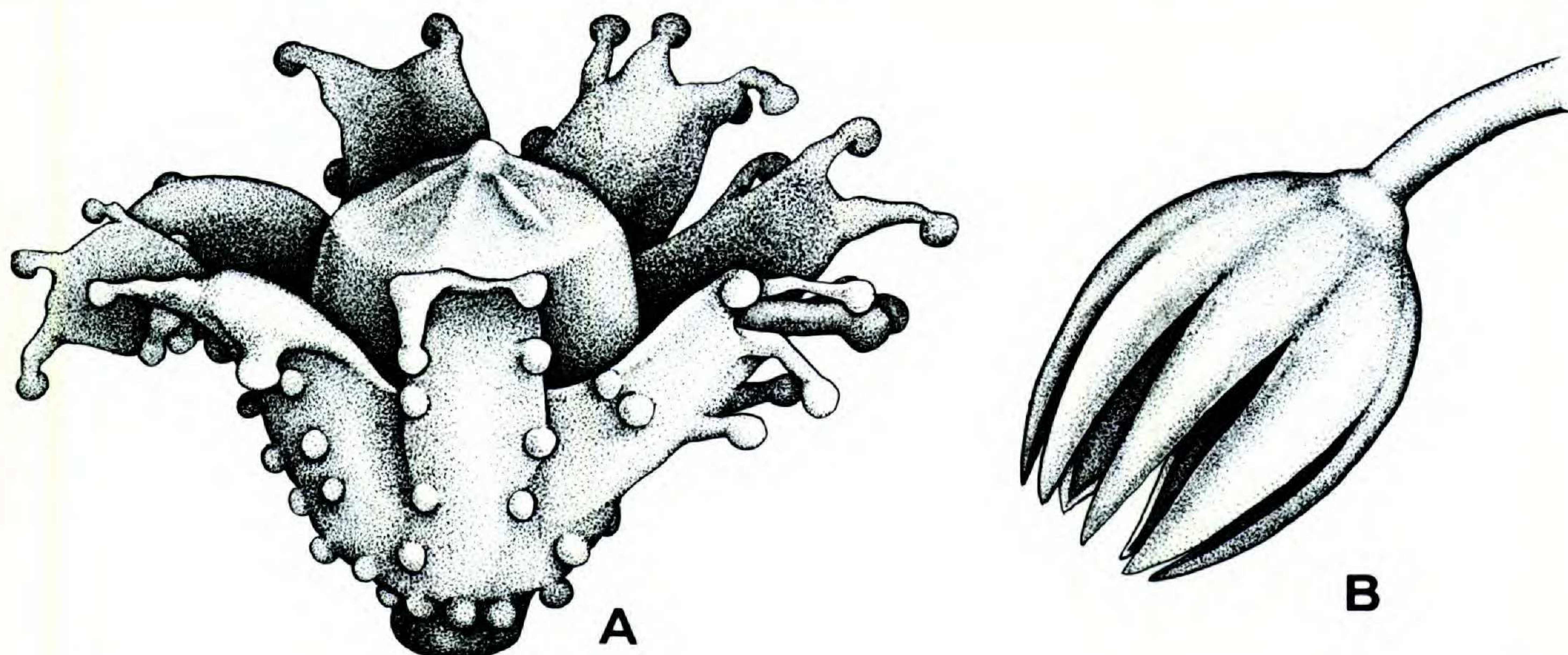


FIGURE 14. Morphology of *Lagenostoma* and *Telangium*. —A. *L. lomaxii*, cupule and ovule, based on Oliver and Scott (1904, text-fig. 2);  $\times 5$ . —B. *T. scottii*, pollen organ, based on Benson (1904, figs. 1, 9, 10);  $\times 7.5$ .

after leaving the stem. On the basis of association and the occurrence of large, distinctive, stalked, capitate glands, *Sphenopteris hoeninghausii* (*Rachiopteris aspera* when anatomically preserved) is thought to be the foliage of *L. oldhamia*.

The ovules of *Lyginopteris* (*Lagenostoma lomaxii*, Fig. 14A) are known attached to *Sphenopteris hoeninghausii* foliage. They were borne terminally on the distal part of the fronds in pedicellate cupules. Each cupule contained a single ovule. The upper half of the cupule bore eight to ten distal lobes, each supplied by a single vascular strand. The ovules were small (about 5.5 mm long) and radiospermic. The single integument was "fused" with the nucellus except near the micropyle. The integument was supplied by eight or nine radially arranged bundles in the endotesta. The megaspore membrane was thick (Oliver & Scott, 1904) and may be up to 5  $\mu\text{m}$  in some lyginopterid pteridosperms (Taylor & Millay, 1981). It is unknown whether the megaspore of *L. lomaxii* had a trilete mark, but this feature does occur in other lyginopterid megaspores (Pettitt, 1969; Schabillion & Brotzman, 1979), and in *Stamnostoma huttonense* there is a cluster of three aborted spores at the apex of the megaspore (Long, 1975). This suggests that lyginopterid megaspores were derived from a tetrahedral rather than linear tetrad.

The microsporangiate organs of *Lyginopteris* are frequently considered to be *Crossothea* (Kidston, 1906; Sporne, 1971a: 55), but there is no evidence linking these two organs as part of the same plant (Jongmans, 1930). *Lyginopteris oldhamia* and *Lagenostoma lomaxii* come from

strata older (Westphalian A) than those in which *Crossothea* is typically abundant. Benson (1904) made a good case for *Telangium scottii* (Fig. 14B) being the *Lyginopteris* microsporangiate organ, based on anatomical similarity and association evidence. *Telangium scottii* comprises bilaterally symmetrical synangia with six to eight ellipsoidal sporangia that dehisced along their inner wall. The pollen (prepollen) was small with a proximal trilete mark. The pollen wall ultrastructure is unknown, but in other supposed lyginopterids (e.g., *Crossothea*, Millay et al., 1978) it is structurally homogeneous. Male gametophyte development is unknown, but presumably germination was proximal and produced motile sperm. The large flagellate spermatozoids described in the micropyle of *Lagenostoma ovoides* (Benson, 1908) would be worth reexamining.

The female gametophyte of *Lagenostoma lomaxii* was cellular, and the development probably involved an initial free nuclear phase followed by centripetal cellularization (McLean, 1912; Oliver & Scott, 1904). The female gametophytes of *L. ovoides* and *Hydrasperma tenuis* were also cellular, and archegonia have been described (Long, 1944; Matten et al., 1984). Long (1975) has described a possible lyginopterid embryo from the Lower Carboniferous of Scotland, but embryos of *Lagenostoma* and all lyginopterid pteridosperms are otherwise unknown.

#### CORDAIXYLON

Several species of microsporangiate and ovulate *Cordaianthus* inflorescences have been de-



scribed in the literature (Rothwell, 1977; Daghlia & Taylor, 1979), but only one is known as part of a "whole plant" (Rothwell & Warner, 1982, 1984). The description given here is based on the *Cordaianthus* inflorescences attached to *Cordaixylon dumusum* stems and leaves from the Late Pennsylvanian of eastern Ohio (Rothwell & Warner, 1982, 1984).

The mature stems were up to about 5 cm in diameter and produced abundant adventitious roots. The plant is reconstructed as a small shrub. The primary vascular system was an endarch eustele, and a bifacial cambium produced secondary xylem and secondary phloem. The secondary xylem was composed of tracheids with crowded multiseriate oval bordered pits on the radial walls. The rays were predominantly uniseriate. Leaves were helically arranged and ranged from needle-like with a single vein to spatulate forms up to 3 cm wide with numerous veins. Some branches bore needle-like leaves at the base and spatulate leaves distally. Others bore needle-like leaves throughout. Anatomical details of the leaves are described by Rothwell and Warner (1984). The stomata consisted of two guard cells with two lateral and two subsidiary cells.

Inflorescences were borne irregularly as epicormic branches on the stems. Frequently the xylem of the cone axis was not continuous with the xylem of the stem. Ovulate inflorescences (*Cordaianthus duquesnensis* Rothwell, 1982b) consisted of a bilaterally symmetrical primary axis bearing four rows of fertile secondary shoots, each in the axil of a bract. The secondary shoots had 60–70 helically arranged scales of which the distal 20–30 were fertile and bore a single terminal ovule. Immature ovules are known attached to the inflorescence and are linked by a continuous morphological series with mature ovules of *Cardiocarpus oviformis* Leisman (1961) that occur in the same deposit. These mature ovules were up to about 9 mm long and distinctly flattened. There was a single integument that was free from the nucellus except at the chalaza. Each ovule was supplied by a single vascular bundle that expanded to form a flattened plate at the base of the nucellus. Below this plate the main vascular bundle produced two lateral traces that ran through the sarcotesta in the primary plane, one on either side of the nucellus. The megaspore membrane was about 5  $\mu$ m thick.

The structure of the microsporangiate inflorescence was similar to that of the ovulate inflo-

rescences, consisting of a bilaterally symmetrical primary axis with four rows of fertile secondary shoots, each in the axil of a bract. The secondary shoots bore helically arranged scales the distal-most of which were fertile. Each fertile scale bore five microsporangia arranged in a ring at the apex. The microsporangia were fused proximally and free distally. Pollen was saccate and of the *Florinites* type. *Florinites* pollen has a distal thinning of the wall and an alveolate wall structure with large cavities.

Nothing is known of cordaite male gametophytes from North American material, but Florin (1936) described male gametophytes from *Florinites* in situ within *Cordaianthus* from Europe (Millay & Eggert, 1974). Florin's material shows axial rows of four or five cells in each grain, and the male gametophyte was therefore basically similar to that seen in many conifers and *Ephedra* (Millay & Eggert, 1974; Fig. 2, see character 1.1). Germination was probably distal (Millay & Taylor, 1974). The female gametophyte of *Cardiocarpus oviformis* was cellular and possessed two archegonia as described in *C. spinatus* by Andrews and Felix (1952). Nothing is known of the embryo of the "*Cordaixylon* plant."

#### MESOXYLON

The cordaite inflorescence *Gothania* was described originally from European material (Scott, 1919), but knowledge of the *Gothania* plant has been increased considerably by description of *G. lesliana* from the Middle Pennsylvanian of Kentucky (Daghlia & Taylor, 1979) and *Mesoxylon priapi* from the Upper Pennsylvanian of eastern Ohio (Trivett, 1983; Trivett & Rothwell, 1985). On the basis of association in both European and North American coal balls, Daghlia and Taylor (1979) suggest that *G. lesliana* is the microsporangiate fructification of a *M. sutcliffi* stem with *Cordaites felicis* foliage and *Mitrospermum compressum* ovules. Trivett and Rothwell (1985) describe *Mesoxylon priapi* based on stems with attached *Cordaites felicis* foliage and microsporangiate inflorescences of the *Gothania* type. This material forms the basis for the description given here.

*Mesoxylon* stems (Beck et al., 1982; Scott & Maslen, 1910) had a primary vascular system consisting of a modified mesarch eustele. A bifacial cambium produced secondary xylem and secondary phloem. The secondary xylem was composed of tracheids with crowded multise-



riate oval bordered pits on the radial walls. The rays were two to four cells wide. Axillary branching is known to occur and axillary buds were covered with needle-like bud scales. The leaves (*Cordaitea felicitis*) were helically arranged, probably spatulate, and several centimeters wide with numerous veins. Anatomical details of the leaves are described by Benson (1912), Good and Taylor (1970), and Trivett and Rothwell (1985). The stomata consisted of two guard cells with two lateral and two subsidiary cells.

Inflorescences were borne in the axils of leaves. Occasionally both an inflorescence and a vegetative bud occur in the axil of a single leaf. Ovulate inflorescences are unknown, but were presumably similar to those of *Cordaixylon dumusum*, consisting of a bilaterally symmetrical primary axis bearing four rows of fertile secondary shoots, each in the axil of a bract. Mature ovules of *Mitrospermum vinculum* (Grove & Rothwell, 1980) occur in the same deposit as *M. priapi* and contain abundant pollen from the *Mesoxylon* plant in the micropyle. Mature ovules were up to about 4 mm long and distinctly flattened. There was a single integument that was free from the nucellus except at the chalaza. The ovule was supplied by a single vascular bundle that expanded to form a flattened plate at the base of the nucellus. Below this the main vascular bundle produced two lateral traces that passed through the sclerotesta and extended to the micropyle in the sarcotesta. The bundles were positioned one on either side of the nucellus in the primary plane of the ovule. The megaspore membrane was 6–13  $\mu\text{m}$  thick.

The structure of microsporangiate inflorescence was similar to that of the ovulate inflorescences, consisting of a bilaterally symmetrical primary axis with four rows of fertile secondary shoots. The secondary shoots had up to 28 helically arranged scales. There were about five fertile scales confined to the distal part of the shoot and each bore four microsporangia arranged in a row at the apex. The microsporangia were free throughout their length. Pollen was saccate and of the *Sullisaccites* type. *Sullisaccites* has a distal monolete or trilete suture and an alveolate wall structure with large cavities (Millay & Taylor, 1974). *Gothania lesliana* produced monosaccate *Felixipollenites* pollen with a monolete or trilete proximal suture. The pollen wall was alveolate, with irregular, medium-sized cavities (Taylor & Daghljan, 1980). Nothing is known of male gametophyte development, but both *Felixipolle-*

*nites* and *Sullisaccites* (prepollen) are thought to have germinated proximally.

Nothing is known of the female gametophyte or embryo of *Mesoxylon*. Male and female gametophytes of other cordaites are known and discussed under *Cordaianthus*.

#### CONIFERS

Possible defining characters of conifers have been discussed already (Fig. 6). The primary vasculature of the stem is eustelic (Beck et al., 1982) with a single bifacial cambium producing secondary xylem and phloem. The secondary xylem is pycnoxylic, characteristically with uniseriate rays, and the tracheids have uniseriate to multiseriate circular bordered pits, generally confined to the radial walls. Some genera have long- and short-shoot systems, and axillary branching occurs. Although there is considerable variation in leaf morphology (see character 3.1), no conifer has pinnate leaves. Stomata are anomocytic (but see Scott & Chaloner, 1983).

Ovulate cones are diverse in form, but all are regarded as fundamentally compound, with cone scales interpreted as fertile shoots in the axils of bracts (see character 3.3). The ovules vary considerably in size and are flattened. Each has a single integument, which frequently has two "horns" on either side of the micropyle in the primary plane (Bierhorst, 1971, figs. 25.3B, 25.3C, 25.5E). These "horns" reflect the ontogenetic development from two opposite primordia that also are positioned in the primary plane (Bierhorst, 1971, fig. 25.5C, 25.5D; Florin, 1951: 364). The integument and nucellus may be "fused" for most of their length or free except at the chalaza. The ovule lacks a well-developed vascular system, and frequently there are no bundles at all (Chamberlain, 1935: 298). The megaspore membrane varies in thickness and complexity of structure. In the Pinaceae and Podocarpaceae it may be 4–6  $\mu\text{m}$  thick, whereas in the Araucariaceae, Cupressaceae, Cephalotaxaceae, Taxaceae, and Taxodiaceae it is generally less well developed and may be extremely thin (Erdtman, 1965). It is also thick in *Lebachia* (Mapes & Rothwell, 1984, pl. 15, fig. 2). Out-group comparison with cycads, *Ginkgo*, and pteridophytes suggests that the thick megaspore membrane is the primitive condition in the conifers, thinner membranes being more specialized. The nucellus and inner lining of the integ-



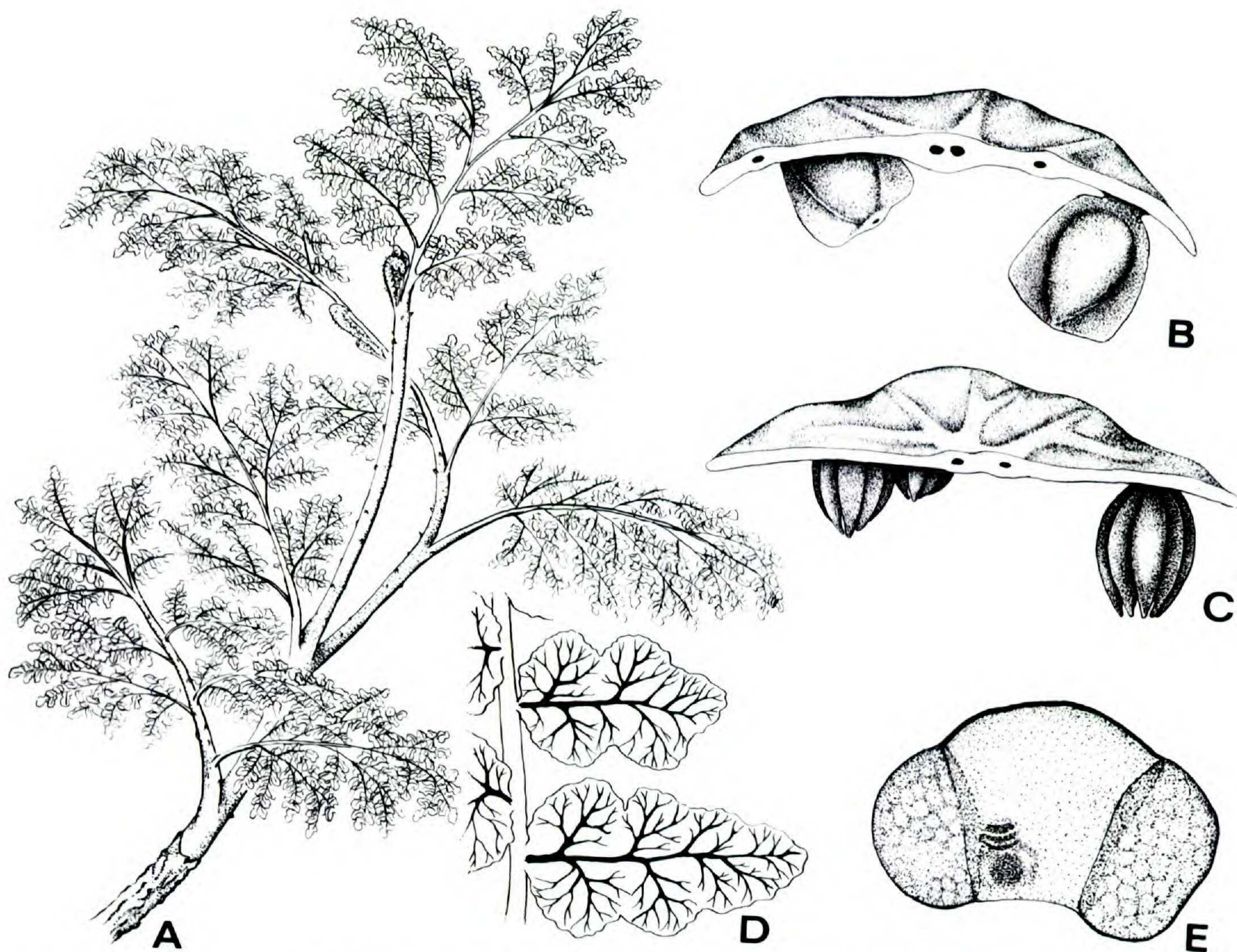


FIGURE 15. Morphology of the *Callistophyton* plant. — A. *Callistophyton*, branch system, redrawn from Rothwell (1975, text-fig. 1);  $\times 0.25$ . — B. *Callospermation pusillum*, fertile pinnule segment bearing two abaxial ovules, based on Rothwell (1981, fig. 3), note that details of seed attachment in *Callistophyton* are not well understood, see text;  $\times 5$ . — C. *Callistophyton*, pinnule bearing three adaxial microsporangiate synangia, based on Rothwell (1981, fig. 3A);  $\times 10$ . — D. *C. boyssettii* detail of proximal pinnules, based on Rothwell (1981, fig. 2B);  $\times 2.5$ . — E. *Vesicaspora* pollen grain from an *Idanotekion glandulosum* pollen sac showing microgametophyte, based on Rothwell (1981, pl. 3, fig. 7);  $\times 900$ .

ument are generally only weakly cutinized (Harris, 1954).

The microsporangiate cones of conifers are extremely variable, but they are all usually considered to be fundamentally simple structures with microsporophylls bearing abaxial microsporangia. There are several kinds of pollen (Erdtman, 1965; Wodehouse, 1935), but saccate grains with a distal aperture are interpreted here as primitive for extant conifers based on out-group comparison with *Lebachia* (see Fig. 6). Saccate pollen is accepted here as primitive for the group. The pollen wall structure in most saccate grains is alveolate with large cavities, but in the non-saccate conifers (e.g., Araucariaceae, Cupressaceae) the pollen wall is granular (Doyle et al., 1975).

Male gametophyte development varies (Sporne, 1971a: 142), but the developmental pattern that occurs in cycads, *Ginkgo*, and *Ephedra*

is accepted here as primitive for the group (see character 1.1). The pollen germinates distally and fertilization is typically siphonogamous, although there are rare reports of zooidogamy in conifers (Christiansen, 1969).

The female gametophyte develops from a single functional megaspore (see character 1.2) that undergoes free nuclear divisions before centripetal cellularization occurs and archegonia are formed. Following fertilization there is a very short free nuclear phase in the development of the embryo.

#### GINKGO

The genus *Ginkgo* contains a single extant species, *G. biloba*, although there are several fossil species, mostly known from foliage only (Trautau, 1968). The primary vasculature of the stem



is eustelic (Beck et al., 1982) with a single bifacial cambium producing secondary xylem and phloem. In long shoots the secondary xylem is pycnoxylic and conifer-like with narrow rays, and uniseriate or biseriate circular bordered pits on the radial walls of the tracheids. Short shoots have manoxylic wood. Axillary branching occurs. The distinctive fan-shaped leaves have two vascular bundles in the petiole. The venation is dichotomous with a few anastomoses (Foster & Gifford, 1974: 449). Stomata are anomocytic.

The ovules are borne in pairs at the end of stalks in leaf axils. The stalks are slightly dorsiventrally flattened and contain two pairs of vascular bundles. Each ovule bearing stalk is interpreted as a short shoot bearing two uniovulate fused megasporophylls each represented by a pair of vascular bundles (Rothwell, pers. comm.). The ovules are large (up to 4 cm long) and either flattened or trigonous. Each has a single, massive integument that frequently has two apical "horns," one on either side of the micropyle in the primary plane (Bierhorst, 1971: 421, fig. 24-4B). There is a sarcotesta, a sclerotesta, and endotesta. The integument and nucellus are "fused" except close to the micropyle. The ovule is supplied by two (or three) poorly developed vascular strands that run inside the sclerotesta to the level at which the integument and nucellus are free. The vascular bundles run in the primary plane, and the sclerotesta has two (or three) distinct ribs. Occasional ovules may have three or four vascular bundles and a corresponding number of ribs. The megaspore membrane is well developed and up to 4–6  $\mu\text{m}$  thick at maturity (Chamberlain, 1935: 208; Erdtman, 1965: 10, but see *Karkenja*, Archangelsky, 1965); the nucellus and inner lining of the integument are only weakly cutinized (Harris, 1954).

The microsporangiate organs also arise in the axils of leaves and consist of a lax inflorescence bearing numerous lateral stalks interpreted here as microsporophylls. Each microsporophyll bears a pair of pendant microsporangia and an apical mucilage-containing "knob" (Sporne, 1971a: 169). At the base of each lateral stalk there is a pair of minute projections. The sporangia dehisce by a single longitudinal slit. The pollen is boat-shaped, non-saccate, and more or less smooth-walled. The pollen wall is alveolate, with large cavities similar to those in many conifers (Zavada & Crepet, pers. comm.). Male gametophyte development is similar to that in *Ephedra* and some conifers (character 1.1). As in cycads,

the final division of the spermatogenous cell produces two large spermatozoids with a spiral band of flagellae (Sporne, 1971a: 170). The pollen germinates distally, produces a haustorial pollen tube, and the motile spermatozoids are released by a rupture in the pollen tube close to the distal pollen wall.

The female gametophyte develops from a single functional megaspore (see character 1.2), which undergoes free nuclear divisions until about 256 nuclei are formed, before cellularization occurs centripetally and archegonia are formed (Sporne, 1971a: 169). Following fertilization, free nuclear divisions produce 256 nuclei before cellularization of the embryo occurs (Chamberlain, 1935: 211; Sporne, 1971a: 171).

#### CALLISTOPHYTON

*Callistophyton* (Fig. 15) is currently the best understood of all seed ferns based on Middle and Upper Pennsylvanian material from North America. Its morphology and reproductive biology are reviewed by Rothwell (1975, 1980, 1981). Stems of *Callistophyton* are up to 3 cm in diameter, and the plant is thought to have been small and shrubby with a scrambling habit (Fig. 15A). The primary vasculature of the stem is eustelic with a pith and a ring of five sympodia, as is typical of *Lyginopteris* and many fossil conifers. The secondary xylem is well developed, typically with biseriate rays but with some up to five cells thick. Tracheids have alternate multi-seriate oval bordered pits on the radial walls. The secondary phloem produced by the bifacial cambium consists of radial files of sieve cells and phloem parenchyma with scattered rays. The stem and all other parts of the plant contained spherical secretory cavities, each lined with an epithelium. Adventitious roots were formed at many of the nodes, and axillary branching occurred. The axillary buds were covered by small linear scales. The leaves (Fig. 15D) were very variable in size, and bi-, tri-, or quadripinnate. They were helically arranged on the stem. The stomata have not been described.

The ovules (*Callospermation*) were borne scattered on the abaxial surface of the leaves (Fig. 15B). Each was flattened with two planes of symmetry. There was a single integument that was free from the nucellus except at the chalaza. It was vascularized by two vascular bundles in the primary plane of the sarcotesta. At the base of



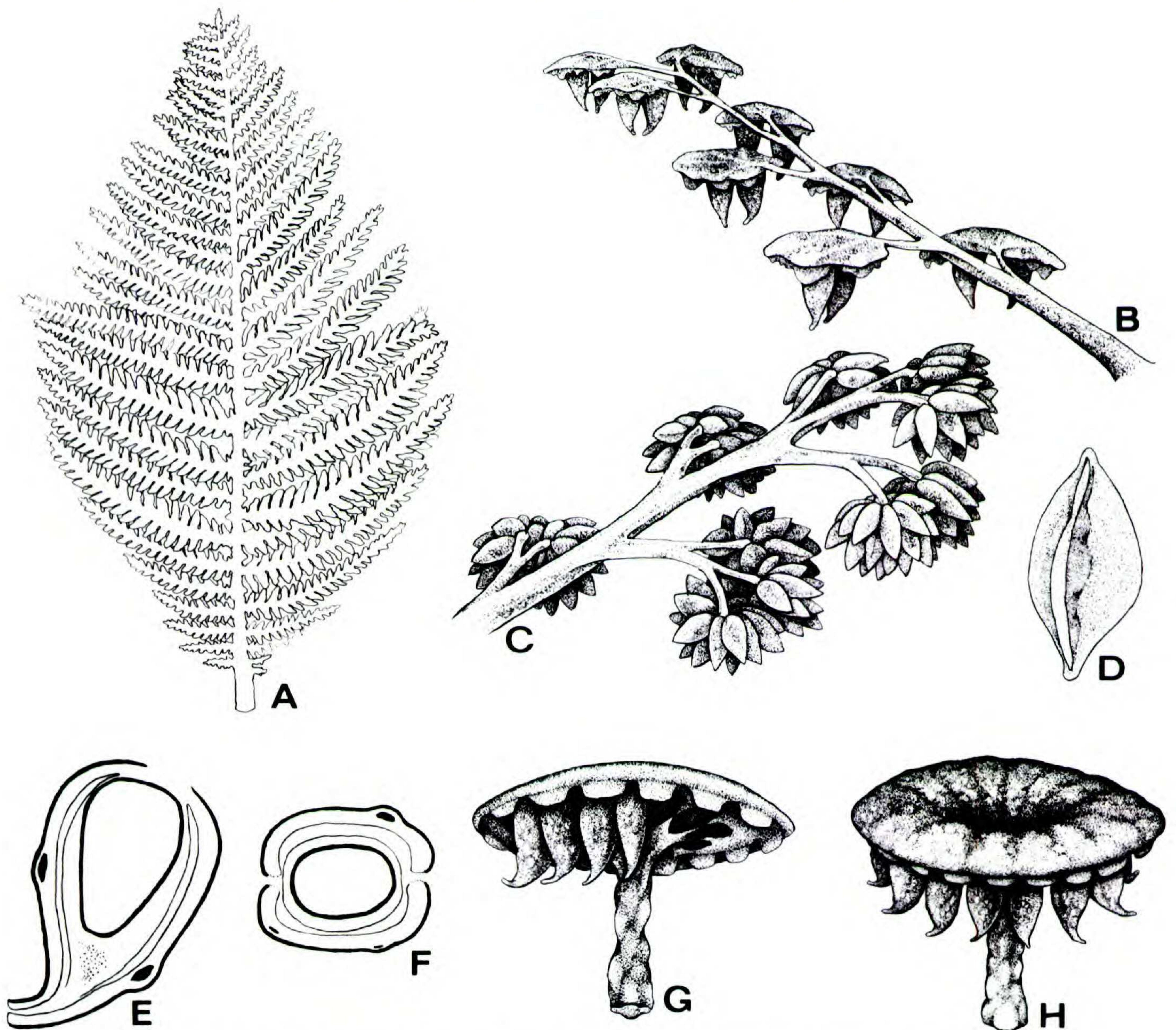


FIGURE 16. Morphology of peltasperms. — A. *Lepidopteris stormbergensis*, bipinnate frond, based on Thomas (1933, fig. 53);  $\times 0.25$ . — B. *Autunia thomasii*, megasporophyll based on Townrow (1960, text-figs. 10B, 11);  $\times 3$ . — C. *Antevsia zeilleri*, based on Harris (1932a, pl. 7, fig. 1);  $\times 2$ . — D. Pollen of *A. zeilleri*, redrawn from Townrow (1960, text-fig. 7J);  $\times 750$ . — E. *Peltaspermum rotula*, longitudinal section of ovule, redrawn from Harris (1932a, fig. 28E);  $\times 4$ . — F. *P. rotula*, transverse section of ovule, redrawn from Harris (1932a, fig. 28E);  $\times 4$ . — G. *P. rotula*, peltate organ bearing a circle of ovules on the lower surface, most ovules removed for clarity, based on Harris (1932a, fig. 28I);  $\times 1.5$ . — H. *P. rotula*, peltate organ bearing ovules on the lower surface, based on Harris (1932a, fig. 28I, pl. 8, fig. 1);  $\times 3$ .

the nucellus there was a distinct disc of vascular tissue. The megaspore membrane was up to 10  $\mu\text{m}$  thick (Rothwell, 1971).

The microsporangiate organs (*Idanothekion*) were radially symmetrical synangia borne abaxially on pinnules (Fig. 15C). Each consisted of six to eight sporangia united for half their length. Distally they formed a tube and dehisced towards the center along a single median suture. The sporangia produced monosaccate pollen of the *Vesicaspora*-type with a distal sulcus (Fig. 15E). The pollen wall is alveolate, similar to that of conifers.

Pollen occurs frequently in the micropyles of *Callospermation* ovules, and a slender, branched pollen tube similar to that of extant conifers has been described (Rothwell, 1972). Germination was distal, and the tube is unlike the larger inflated haustorial structures of extant cycads and *Ginkgo* (Rothwell, 1980: 92). It seems likely that the *Callistophyton* pollen tube indicates siphonogamy. *Vesicaspora* pollen has been described with cellular contents preserved, and the four-celled axial row has been interpreted as three prothallial cells with a larger antheridial cell (Rothwell, 1981: 114). Microgametophyte development was



TABLE 7. Isolated organs of the three better understood peltasperms (after Townrow, 1960; Kerp, 1982).

| Locality                              | Leaf                               | Megasporophyll              | Microsporophyll          |
|---------------------------------------|------------------------------------|-----------------------------|--------------------------|
| South Africa<br>(M. Triassic)         | <i>Lepidopteris stormbergensis</i> | <i>Autunia thomasii</i>     | <i>Antevsia extans</i>   |
| Sweden & E Greenland<br>(U. Triassic) | <i>Lepidopteris ottonis</i>        | <i>Peltaspermum rotula</i>  | <i>Antevsia zeilleri</i> |
| Nahe, West Germany<br>(L. Permian)    | <i>Callipteris conferta</i>        | <i>Autunia milleryensis</i> | —                        |

therefore basically similar to that in *Ephedra*, some conifers, and cordaites (*Florinites*, Millay & Eggert, 1974; see character 1.1).

Megagametophyte development is thought to have involved free nuclear divisions, followed by centripetal cellularization and differentiation of two archegonia. Cellular embryos have not been recognized.

PELTASPERMS

The Peltaspermaceae range from the Lower Permian to Upper Triassic and are known from leaves (*Callipteris conferta*, *Lepidopteris*), microsporophylls (*Antevsia*), and megasporophylls (*Autunia*, *Peltaspermum*) (Fig. 16) (Antevs, 1914; Harris, 1932a, 1937; Kerp, 1982; Lundblad, 1950; Mamay, 1975, 1978; Salmenova, 1979; Thomas, 1933; Townrow, 1960). Two species are known from all three organs (Table 7). The individual organs never have been found connected, but they all show highly characteristic blister-like swellings of the cuticle. This and other cuticular similarities, combined with association, provide evidence to link them together.

Almost nothing is known of the stem of the peltasperms (Townrow, 1960: 340), but the leaves apparently were deciduous, and this suggests that the plants were woody. The leaves were bipinnate (Fig. 16A) with bulbous frond bases. Pinules were borne both on the pinnae and directly on the leaf rachis. Stomata were anomocytic.

Four species of megasporophylls have been described (Kerp, 1982): *Autunia dzungaricum* (*Peltaspermum dzungaricum* Salmenova, 1979); *A. milleryensis*; *A. thomasii* (*P. thomasii*, Harris, 1937; Thomas, 1933; Townrow, 1960); and *P. rotula* (Harris, 1932a). They were dorsiventrally organized and branched in a single plane (Townrow, 1960). It is not known how they were attached to the plant. Each lateral “branch” (interpreted here as a pinna of the megasporophyll) terminated in a swollen lamina that bore seeds on the lower surface. In *A. dzungaricum*, *A. mil-*

*leryensis*, and *A. thomasii* the lamina bore two seeds lateral to the insertion of the “branch” (Fig. 16B). In *P. rotula* the seed bearing lamina was peltate with the “branch” inserted centrally to the undersurface: ten to 12 seeds were arranged around the insertion of the “branch” (Fig. 16G, H). The lobed margin of the lamina in *P. rotula* was reflexed and attached to the “branch.” Only the ovules of *P. rotula* are known in detail (Fig. 16E, F). They were flattened and unitegmite with a long, bilobed, micropylar tube. The cuticle of the outer integument separated into two halves on maceration (Harris, 1932a: 69), and I interpret this as reflecting a platyspermic organization of the seed. Nothing is known of seed vasculature. The nucellus was free from the integument except at the base. The megaspore membrane was thick and resistant to maceration.

Microsporophylls (*Antevsia*) were bipinnate, with alternate primary branching in one plane (Fig. 16C). It is not known how they were attached to the plant. Secondary branching was irregular and frequently at 90° to that of the primary branching. Secondary branches were short and bore four to 12 unilocular, pendulous pollen sacs that dehisced along a single longitudinal suture. Pollen was ellipsoidal, non-saccate, with a single distal sulcus (Fig. 16D). Fine structure of the pollen wall is unknown.

Nothing is known of the gametophytes or embryo of peltasperms.

GLOSSOPTERIDS

An outline cladogram of glossopterids has been presented already (Fig. 8); only additional features thought to be general for the group are mentioned here.

The *Glossopteris* plant is thought to have been a large tree (Gould & Delevoryas, 1977; Pant, 1977a). The primary vasculature was eustelic, and a bifacial cambium produced secondary phloem and large amounts of secondary wood (*Araucarioxylon*). The wood was pycnoxylic, with



tracheids with multiseriate opposite or alternate circular bordered pits. The rays were uniseriate. Secondary xylem of identical structure is known to have been produced in the roots (*Vertebraria*, Gould, 1975). Axillary branching is known to have occurred. The leaves were borne in whorls or spirals, probably on long and short shoots (Pant, 1977a). The leaves were simple and narrowly elliptical with a midrib and well-developed reticulate venation (character 4.1). Stomata were anomocytic.

The ovules were borne on different kinds of megasporophylls (see characters 4.2, 4.5) in the axil of a leaf. The ovules of the silicified Australian material (Gould & Delevoryas, 1977) were not described in detail, but they appear to have been pyriform, and some appear flattened (Gould & Delevoryas, 1977, fig. 7c). Those associated with permineralized Antarctic *Glossopteris* material (Schopf, 1976: 56–57) were distinctly platyspermic, and the vasculature was probably “similar to cordaitan ovules” (Schopf, 1976: 57). The *Glossopteris* ovules described from compressions (e.g., *Pterygospermum*, Pant & Nautiyal, 1960) also were flattened, with a single integument and a long micropylar tube. The integument and nucellus were apparently free except at the chalaza. The nucellar cuticle was robust, but a megaspore membrane up to 6  $\mu\text{m}$  thick also was present (Pant & Nautiyal, 1960).

The microsporophylls were borne adnate to a *Glossopteris* leaf (character 4.3). The sporangia (*Arberiella*) had a finely striated wall and dehiscence by a single longitudinal slit. They produced saccate pollen of the *Protohaploxypinus* type with a distal sulcus. The wall structure of glossopterid pollen has not been studied in detail but is interpreted here as probably alveolar, similar to that of many conifers and cordaites.

Nothing is known of the male gametophyte, but germination apparently was distal. Limited information is available, however, concerning the female gametophyte, which was apparently cellular and contained either one (Gould & Delevoryas, 1977: 392) or two archegonia (Schopf, 1976: 56). The embryos of *Glossopteris* are unknown.

#### CAYTONIA

*Sagenopteris* leaves range from the Upper Triassic to Upper Cretaceous (Harris, 1951b, 1964), but knowledge of the *Caytonia* plant is based on a limited number of localities in east

Greenland (Harris, 1933, 1937), eastern U.S.S.R. (Krassilov, 1977a), Poland (Reymanówna, 1973), Sardinia (Edwards, 1929), Sweden (Lundblad, 1948), and most importantly the Middle Jurassic of England (Thomas, 1925; Harris, 1940a, 1940b, 1941, 1945, 1951b, 1958, 1964). Three similar species are known from leaves, microsporophylls, and megasporophylls (Fig. 17, Table 8). The organs have never been found organically connected but are linked by association evidence, similarity of cuticular structure, and the consistent occurrence of *Caytonanthus* pollen in the micropyles of *Caytonia* ovules (Thomas, 1925; Harris, 1933, 1940a, 1941, 1951b, 1964). Other genera of reproductive structures that may be related to *Caytonia* (e.g., *Pramelreuthia* Kräusel, 1949; *Ktalenia* Archangelsky, 1963) are not included in this discussion of characters.

The stem of the *Caytonia* plant is known from several small twigs (Harris, 1940b, 1971), but they are sufficient to show that it was a woody shrub or tree with alternate leaves. The twigs were thicker than in most extant temperate trees and shrubs. They bore alternating zones of bud-scales and leaves. Buds occur in the axils of the leaves. Branching was sympodial, the apical bud ceasing to grow and being succeeded by two lateral buds to give forked branching as occurred for example in the bennettitalean *Wielandiella angustifolia* (Nathorst, 1909). The leaves (*Sagenopteris*, Fig. 17A, B) were borne on raised “leaf cushions” and had a long petiole bearing four narrowly elliptical leaflets at the apex. Although superficially palmate, the leaflets were arranged in two pairs (Fig. 17B). They each have a midrib and reticulate venation. Small leaves with broad stipule-like petiolar flanges and bud-scales also are known (Harris, 1940b). The leaves apparently were deciduous, with both leaflets and petioles shed. Stomata were anomocytic.

The megasporophylls (*Caytonia*, Fig. 17E) were pinnate, bearing lateral “cupules” on short stalks. It is not known how they were attached to the stem. The “cupules” were reflexed, with a small lip on one side close to the stalk. They were all borne on one surface of the rachis, and all were reflexed in the same direction. Differentiation of the cuticle suggests that the lips were on the upper (presumed adaxial) surface (Harris, 1940a). The cells around the lip were papillate (Thomas, 1925: 310). At maturity the “cupules” probably were fleshy and “berry-like” (Harris, 1951b) and shed individually. The “flesh” of the “cupule” consisted of a network of vascular strands, large



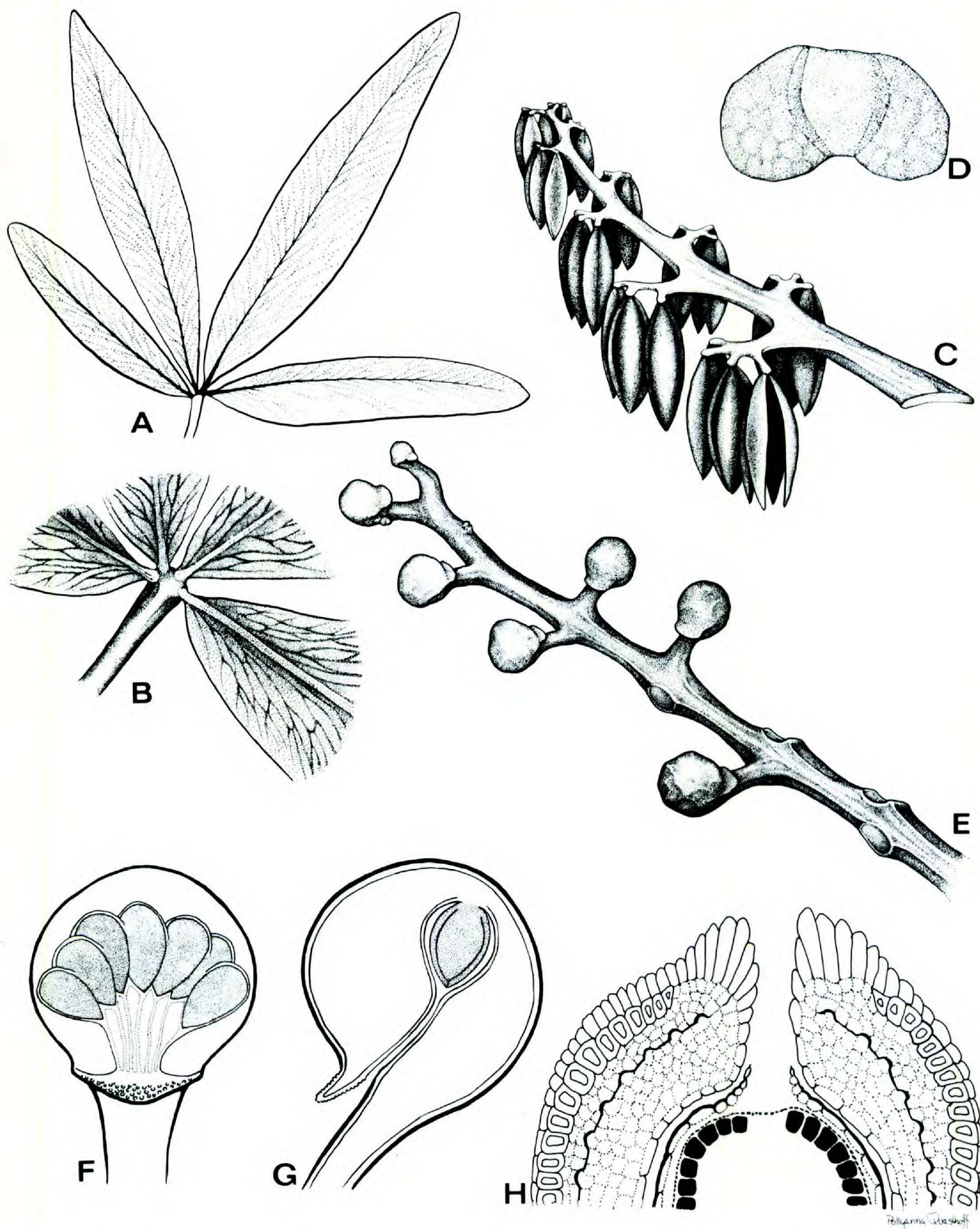


FIGURE 17. Morphology of the *Caytonia* plant.—A. *Sagenopteris colpodes*, based on Thomas (1925, pl. 15, fig. 50);  $\times 0.75$ .—B. *S. colpodes*, detail of leaflet attachment and venation, based on Harris (1964, fig. 2H);  $\times 4$ .—C. *Caytonanthus arberi*, based on Harris (1941, pl. 2, fig. 3);  $\times 7$ .—D. Pollen from *C. arberi*, based on Townrow (1962b, fig. 3d, e);  $\times 1,200$ .—E. *Caytonia nathorstii* megasporophyll, based on Harris (1964, fig. 10A–C);  $\times 5$ .—F. *Caytonia* “cupule” containing seeds, based on Reymanówna (1973, particularly text fig. 12E, F);  $\times 12.5$ .—G. *Caytonia* “cupule,” longitudinal section, based on Reymanówna (1973, particularly text-fig. 12E, F);  $\times 12.5$ .—H. *C. nathorstii* ovule longitudinal section, redrawn from Harris (1958, fig. 7);  $\times 110$ .



TABLE 8. Isolated organs of the three best known species of the *Caytonia* plant (after Harris, 1941, 1951b).

| Locality                                 | Leaf                | Megasporophyll    | Microsporophyll     |
|------------------------------------------|---------------------|-------------------|---------------------|
| U.K., Yorkshire<br>(M. Jurassic)         | <i>Sagenopteris</i> | <i>Caytonia</i>   | <i>Caytonanthus</i> |
|                                          | <i>colpodes</i>     | <i>sewardi</i>    | <i>oncodes</i>      |
|                                          | <i>Sagenopteris</i> | <i>Caytonia</i>   | <i>Caytonanthus</i> |
| E Greenland<br>(U. Triassic–L. Jurassic) | <i>phillipsii</i>   | <i>nathorstii</i> | <i>arberi</i>       |
|                                          | <i>Sagenopteris</i> | <i>Caytonia</i>   | <i>Caytonanthus</i> |
|                                          | <i>nilssoniana</i>  | <i>thomasii</i>   | <i>kochii</i>       |

rounded cells, and branched sclereids (Reymańówna, 1973). Each “cupule” contained a “packet” of several small ovules surrounded by a common cuticular membrane that was continuous with the outer cuticle of the cupule (Fig. 17F; Krassilov, 1977a; Reymańówna, 1973). The ovules were arranged with their micropyles oriented towards the mouth, below the lip of the “cupule.” Narrow channels ran between the cuticles of the mouth connecting the micropyles with the outside (Fig. 17G).

The ovules were flattened and unitegmic, with a narrow micropylar slit (Harris, 1940a, 1958; Thomas, 1925). The integument was free from the nucellus except at the chalaza and was supplied by a pair of vascular bundles (Reymańówna, 1973). Each bundle consisted of scalariform tracheids that ran along the edge of the seed in the primary plane, almost to the micropyle. The integument and nucellus were strongly cutinized, but no acid-resistant megaspore membrane was detected (Fig. 17H; Harris, 1958).

The microsporophylls (*Caytonanthus*, Fig. 17C) were pinnate, with irregular, short, lateral “branches.” It is not known how they were attached to the plant, but they were dorsiventrally flattened, with different cuticles on the upper and lower surfaces. On their lower surface the lateral “branches” bore radially symmetrical, elongated synangia, with four (rarely, three or five) locules. The locules dehisced longitudinally towards the inside, separating in the middle but remaining attached at the apex and base. The pollen (*Vitreisporites*, Fig. 17D) was bisaccate with a distal sulcus. Krassilov (1977a) has described monosaccate grains. The pollen wall was alveolate with large cavities (Crepet & Zavada, pers. comm.). Although *Caytonia* was claimed originally to be an angiosperm (Thomas, 1925), Harris (1933, 1940a) demonstrated *Vitreisporites* pollen in the micropyles of *Caytonia* seeds. Pollination probably involved a pollination drop mechanism that drew pollen along the channels of the mouth and onto the micropyles.

Nothing is known of the male or female gametophyte of *Caytonia*, and the embryo is only known from “aleurone cells” (Harris, 1958).

CORYSTOSPERMS

The Corystospermaceae was established by Thomas (1933) for leaves, microsporophylls, and megasporophylls from the Middle Triassic Molteno Beds of the Upper Umkomaas Valley, Natal (see Anderson & Anderson, 1983). Some of Thomas’ specimens have been subsequently reinterpreted (Townrow, 1962a), and additional material has been described from the Molteno flora of Zimbabwe (Lacey, 1976), the Upper Triassic/Lower Jurassic of Tasmania (Townrow, 1965), the Triassic of New South Wales (Holmes & Ash, 1979), the Triassic of India (Pant & Basu, 1973, 1979; Srivastava, 1974), the Triassic of Argentina (Archangelsky, 1968; Petriella, 1979, 1980, 1981, 1983), and the Middle Jurassic of Yorkshire (Harris, 1964). The individual organs have never been found in organic connection but are treated together on the basis of consistent association, similarity of cuticular structure, and the occurrence of pollen from the microsporangia in micropyles of the ovules (Archangelsky, 1968; Harris, 1964; Thomas, 1933; Townrow, 1962a, 1965).

The corystosperms were woody plants, but their stems are poorly known. Harris (1983a) described the stem of *Pachypteris papillosa* based on compressions, and Archangelsky (1968) has suggested that *Rhexoxylon* (Fig. 18G; Archangelsky, 1968; Archangelsky & Brett, 1961) may be the stem of some Triassic corystosperms. Externally *Rhexoxylon* showed leaf bases and branch scars. It is not known whether axillary branching occurred. Internally there was a large pith surrounded by a ring of vascular segments with secondary xylem developed both centripetally and centrifugally in relation to the primary xylem. This “polystelic” arrangement may well be merely a modification of a basic eustele (Beck et al.,



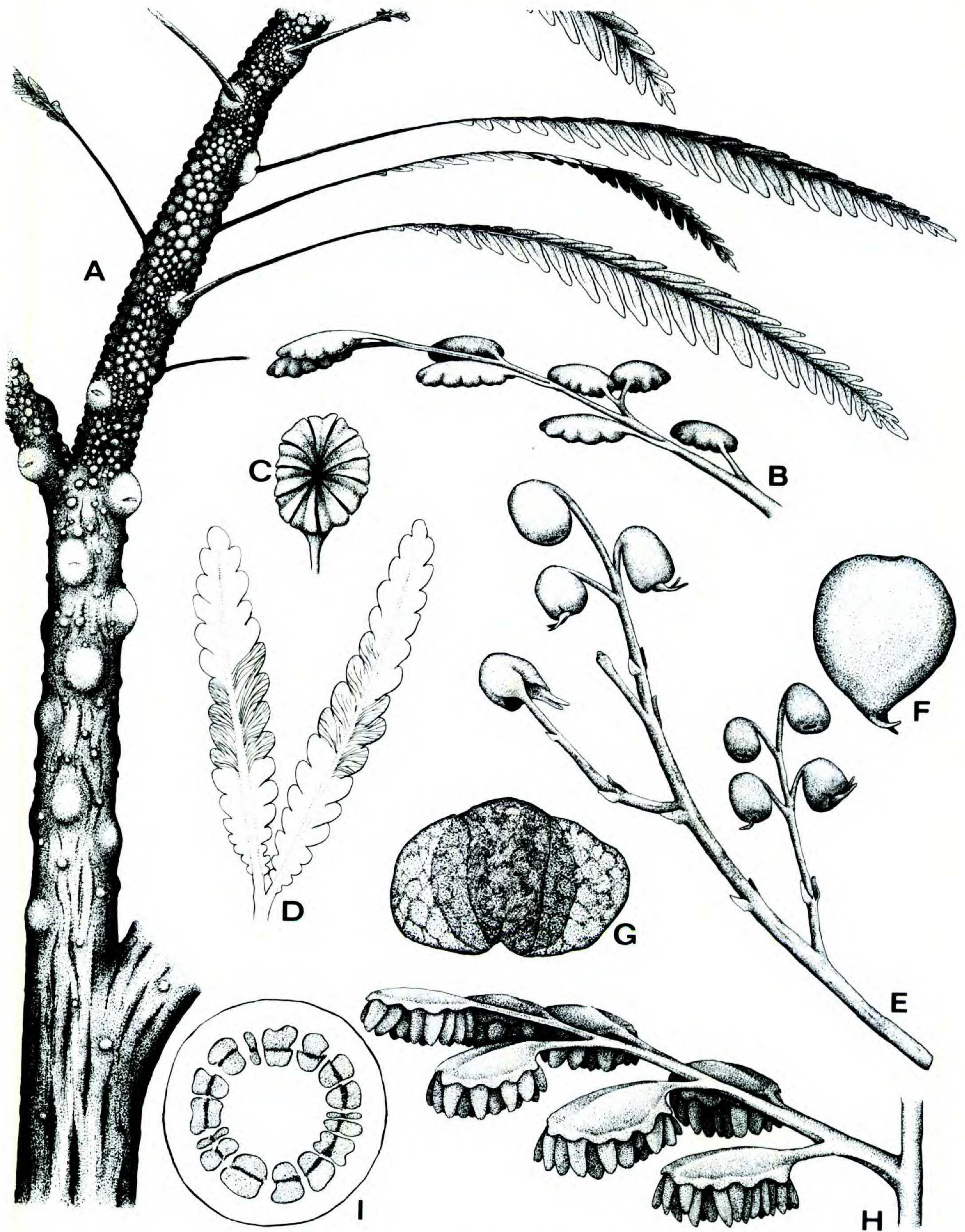


FIGURE 18. Morphology of corystosperms.—A. *Pachypteris papillosa* stem with leaves, based on Harris (1983a, fig. 2);  $\times 0.25$ .—B. *Pteroma thomasii* synangium, abaxial view, redrawn from Harris (1964, fig. 66B);  $\times 2.5$ .—C. *P. thomasii*, lateral view, based on Harris (1964, fig. 66A–G, I);  $\times 2$ .—D. *Dicroidium odontopteroides*, redrawn from Thomas (1933, fig. 49a);  $\times 0.75$ .—E. *Umkomasia macleanii*, redrawn from Thomas (1933, fig. 1, pl. 26, fig. 56);  $\times 2.5$ .—F. Corystosperm ovule based on Thomas (1933, fig. 33c);  $\times 4$ .—G. *Rhexoxylon*, transverse section of stem, based on Archangelsky and Brett (1961, fig. 2A);  $\times 0.5$ .—H. Pollen of *Pteruchus africanus*, redrawn from Townrow (1962a, fig. 10F);  $\times 600$ .—I. *P. africanus*, based on Townrow (1962a, fig. 1A–D);  $\times 2.5$ .



1982; Stewart, 1983). The primary xylem contains tracheids with spiral thickenings or scalariform pitting. The secondary xylem segments were pycnoxylic, although some axial parenchyma occurred. The tracheids had uniseriate to triseriate, circular bordered pits on the radial walls. The rays were uniseriate (Archangelsky & Brett, 1961).

Corystosperm leaves have been referred to a variety of genera, including *Dicroidium* (Fig. 18D), *Xylopteris*, and *Pachypteris* (Townrow, 1965). The leaf rachis was generally forked, with a simple or bipinnate arrangement of pinnae (Retallack, 1977: 255; Townrow, 1965). Stomata were anomocytic.

Megasporophylls were dorsiventrally organized and branched in a single plane (Fig. 18E). They consisted of a main axis with irregularly positioned lateral "branches" bearing several recurved "cupules." Thomas (1933) described "bracts" and pairs of "bracteoles" on these structures, and he therefore interpreted them as fertile branches. However, a similar interpretation of the microsporangiate organs was not supported by Townrow (1962a), who showed the "bracts" to be sterile pinnules. The "cupule"-bearing structures never have been reinvestigated but are interpreted here as megasporophylls. It is not known how they were attached to the stem.

The megasporophylls were highly variable, and Thomas (1933) recognized three genera, based on branching pattern, the form of the "cupule," and the presence or absence of cupular hairs. In *Umkomasia* the "cupules" were divided into two lobes by clefts in the plane of branching, and lacked hairs or hair bases on the inner surface. *Pilophorosperma* had "cupules" with a single cleft and their inner surface covered by hairs. *Spermatocodon* had "cupules" with no conspicuous clefts, which lacked hairs on the inner surface. In all three genera each "cupule" contained a single ovule. Other subsequently described corystosperm "cupules" (e.g., *Karibacarpon*, Lacey, 1976; Holmes & Ash, 1979) also contain a single ovule.

The ovules were flat (Fig. 18F), and although their vasculature is unknown, they had files of small rectangular cells arranged in longitudinal rows along their two margins (Thomas, 1933: 229). At their apex the ovules had two elongated micropylar lobes that were curved to one side in the primary plane. The curved micropylar tube was oriented away from the cupule stalk. Detailed observations on the seed membranes of

corystosperms still are needed, but Thomas (1933: 228) noted "a well cutinized testa" and an "exceedingly delicate inner membrane." The ovules are assumed to have been unitegmic, and the megaspore membrane probably was not well developed.

Microsporophylls (*Pteruchus*, Fig. 18I) were branched irregularly and bore groups of pendulous pollen sacs on expanded distal laminae. The "branches" (rachises, Townrow, 1962a) were attached either in a single plane (Townrow, 1962a) or spirally (Pant & Basu, 1973, 1979; Srivastava, 1974; Thomas, 1933). It is not known how the main axis was attached to the plant. Townrow (1962a) emphasized the leaf-like nature of *Pteruchus*, and it is interpreted here as a microsporophyll. Pollen sacs were ellipsoidal, unilocular, and dehiscent along a single suture. Pollen was bisaccate (Fig. 18H), with a single distal sulcus, and very similar to that produced by *Caytonanthus* (Townrow, 1962b). The pollen wall was granular (Crepet & Zavada, pers. comm.; see also Taylor et al., 1984). Pollen has been described in the micropyle of one of the South African ovules (Thomas, 1933).

The microsporophyll *Pteroma thomasi* Harris (Fig. 18B, C) from the Middle Jurassic of Yorkshire also is included in the Corystospermaceae by Townrow (1965). On the basis of association and some similarity in cuticle, it is thought to be part of the *Pachypteris papillosa* plant (Harris, 1964). *Pteroma* is a pinnate structure with oval or round fertile laminae with a ring of microsporangia embedded in their undersurface. The microsporangia were unilocular, dehiscent by a single longitudinal slit and produced bisaccate pollen.

Nothing is known of the male or female gametophyte, or embryo of corystosperms.

#### PENTOXYLON

Knowledge of the *Pentoxylon* plant is based mainly on silicified material from the Jurassic of the Rajmahal Hills, India. Sahní (1948) gave the most detailed account and linked the ovulate heads (*Carnoconites*) with the stem (*Pentoxylon*, Fig. 19D) and the leaves (*Nipaniophyllum*, Fig. 19C) on the basis of association evidence and structural similarity. Microsporangiate organs (*Sahnia*, Fig. 19E) were described subsequently by Vishnu-Mittre (1953), and knowledge of the *Pentoxylon* plant was reviewed by Rao (1976, 1981). The other published reports of *Pentoxy-*



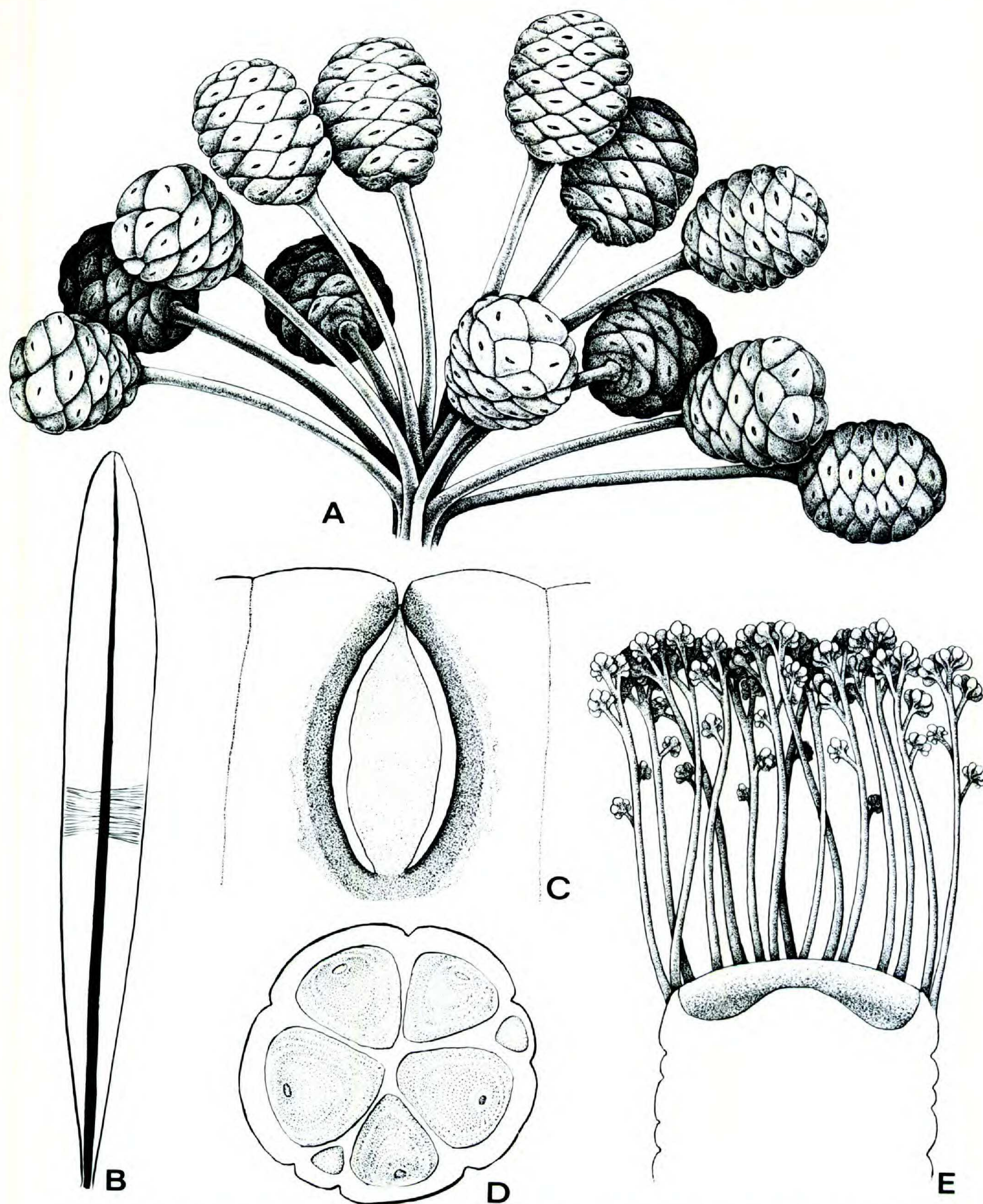


FIGURE 19. Morphology of *Pentoxylon* plants.—A. *Carnoconites cranwelliae*, ovulate heads, based on Harris (1962, text-fig. 2B, fig. 1);  $\times 2.5$ .—B. *Carnoconites*, longitudinal section through ovule, based on Sahni (1948, fig. 21);  $\times 10$ .—C. *Nipaniophyllum raoi*, redrawn from Sahni (1948, fig. 34a, b);  $\times 1$ .—D. *Pentoxylon sahnii*, transverse section of stem showing vascular strands, based on Sahni (1948, fig. 9);  $\times 8$ .—E. *Sahnia* microsporangiate "flower," based on Vishnu-Mittre (1953, fig. 11) and Bose et al. (in press);  $\times 2.5$ .

*lon* are based on ovulate heads (Fig. 19A) and leaves preserved as compressions from the uppermost Jurassic or lowermost Cretaceous of New Zealand (Harris, 1962, 1983b) and a variety of different organs in the early Cretaceous of Vic-

toria (Drinnan & Chambers, 1985), New South Wales (White, 1981), and Queensland, Australia (Turner, pers. comm.). The description given below and used in the phylogenetic analysis is based on both the silicified and compression material.



The stem (*Pentoxylon*) was differentiated into long and short shoots, both with helically arranged leaf-cushions showing leaf scars. In transverse section the stem typically had five vascular segments, but as in medullosans this is interpreted as a modification of a fundamentally eustelic arrangement (Beck et al., 1982: 749; Stewart, 1976). The secondary xylem was pycnoxylic with uniseriate rays and no axial parenchyma. Secondary xylem tracheids had uniseriate or biseriate circular bordered pits on their radial walls, although scalariform pitting has been reported in the microsporangiate structures and short shoots of *Sahnia* (Vishnu-Mittre, 1953). Leaf-traces arose in pairs, one from each of two adjacent vascular segments (Stewart, 1976). The leaves (*Nipaniophyllum*) were simple, strap-shaped, and of the taeniopterid-type, with a midrib and numerous pinnate veins. Stomata were originally described as "fundamentally Bennettitalean" (Sahni, 1948: 56), but many are apparently anomocytic, and the morphology and ontogeny of the stomata require detailed reexamination (Rao, 1976).

The ovules were sessile, orthotropous, helically arranged, and aggregated into compact ovoid (*Carnoconites compactum*, *C. cranwelliae*) or elongated heads (*C. laxum*). Each head of *C. compactum* consisted of about 20 ovules, but there were more in *C. cranwelliae* and *C. laxum*. No bracts or other structures were associated with these heads, nor were there interseminal scales as in Bennettitales. The ovulate heads were borne terminally on short shoots. In the Indian material a single pedicel produced several branches, each of which bore a single ovulate head. In the New Zealand material (*C. cranwelliae*) 12 separate pedicels arose from the same point in an umbel-like arrangement, and each bore a single ovulate head.

Ovules of *Carnoconites compactum* were flattened, with two integuments that were free from the nucellus except at the chalaza. The sclerotesta was bicarinate and distinctly flattened in transverse section. Immediately surrounding the sclerotesta was a distinct layer of dark cells. The remaining outer part of the "integument" formed a thick, fleshy "sarcotesta" interpreted here as an outer integument and probable "cupule" homologue (see character 9.19). Each ovule was supplied by a single vascular bundle that penetrated the sclerotesta at the chalazal end; no other vascular tissue has been reported in the ovules.

The ovule cuticles of *C. compactum* and *C. laxum* are unknown, but in *C. cranwelliae* the sarcotesta had a thick outer cuticle. The inner cuticle of the integument was delicate but the nucellar cuticle was robust. There was no megaspore membrane preserved.

The microsporophylls (*Sahnia*) were borne in a whorl, or low helix, forming a "flower" around a broad, conical, sterile receptacle. They were surrounded themselves by deciduous bracts. According to Vishnu-Mittre (1953), the microsporophylls were fused proximally to form a shallow cup, but according to Rao (1981), they were free at the base. The microsporophylls were numerous, and each bore ten to 20 spirally arranged, stalked unilocular sporangia. The sporangia were borne singly or in groups of two or four. Each sporangium was pyriform and thick-walled, with monosulcate non-saccate pollen. Pollen wall stratification was probably granular (Taylor & Crane, in progress).

Monosulcate pollen has been described in the micropyles of *Carnoconites* ovules. Germination was apparently distal. Nothing is known of the male gametophyte, and Sahni (1948: 46) describes one poorly preserved specimen with what may be the remains of megagametophyte tissue. No well-preserved embryos have been described, although Harris (1962) mentions a flat, cutinized plate in *C. cranwelliae* seeds, which he tentatively interpreted as the remains of the "aleurone layer" of the "endosperm."

#### BENNETTITALES

An outline cladogram of the Bennettitales already has been presented (Fig. 12). Knowledge of other characters is very uneven, and in this section a general description of the Bennettitales is synthesized from features preserved in the different taxa.

The Bennettitales exhibited considerable diversity in habit ranging from unbranched pachycaul forms (*Cycadeoidea*, *Monanthesia*) to forms that were more slender and highly branched (Delevoryas, 1975; *Ischnophyton*, Delevoryas & Hope, 1976; *Williamsonia leckenbyi* plant, Harris, 1969). The anatomy of highly branched forms is unknown, but in pachycaul plants there was a large pith and a single broad ring of vascular tissue. The primary vasculature was eustelic, and a bifacial cambium produced both secondary xylem and secondary phloem. The wood was dis-



sected into numerous segments by broad rays, but individual segments were pycnoxylic with only uniseriate or biseriate rays. Tracheidal pitting was highly variable (Bose, 1953) ranging from multiseriate circular bordered pits to scalariform pitting (Sahni, 1932a). Leaf-traces pass directly into the leaf and do not girdle the stem as in cycads (Crepet, 1974: 178). Axillary branching is known to have occurred. Leaves generally were pinnate (see character 6.10) although there was some variation (Ash, 1975), and in *Eoginkgoites* there were several pairs of pinnae at the apex of the petiole giving a pseudopalmate arrangement (Ash, 1976, 1977). Stomata were paracytic, with distinctive cuticular thickenings (see character 6.2).

Ovules were grouped into "flower-like" heads, generally with surrounding bracts forming a "perianth" (but see *Vardekloeftia*, character 6.5). The ovules were small, generally less than 7 mm long, and frequently only 1–2 mm. Ovules were radially symmetrical (although flattened in *Vardekloeftia* and *Bennetticarpus wettsteinii*), with two integuments that were free from the nucellus except at the chalaza (see p. 764). Frequently the nucellus was borne on a long stalk. Each ovule was supplied by a single vascular trace that ran to the base of the nucellus, but no other vasculature is known in the integument. Distally the integument was elongated into a long micropylar tube, and at maturity the integument was differentiated into four layers (Crepet, 1974: 157). The megaspore membrane was thin or not acid-resistant, but the cuticle of the nucellus and inner surface of the integument was well cutinized (Harris, 1954, 1969). The ovules were not individually subtended by any other organs but are surrounded by numerous sterile interseminal scales that develop from primordia of bitegmic ovules (see character 6.1). The interseminal scales generally have a single vascular bundle.

Microsporophylls were aggregated into "flower-like" heads surrounded by a "perianth" of bracts. The microsporangia are borne in various ways, but most of those known are aggregated into bivalved synangia (character 6.4). Pollen is monosulcate, boat-shaped, and more or less smooth-walled. The pollen wall is granular (*Cycadeoidea*, Crepet, pers. comm.; Taylor, 1973).

The multicellular male gametophytes reported by Wieland (1906) are now interpreted as internal folds in the pollen wall (Taylor, 1973). The female gametophyte apparently was monosporic, developing from the innermost of a linear tetrad

of megaspores (*Cycadeoidea*, Crepet & Delevorayas, 1972). Little is known of the subsequent development in *Cycadeoidea*, but according to Sharma (1974), in *Williamsonia* free nuclear divisions were followed by cellularization beginning at the micropylar end and proceeding toward the base. Cellular dicotyledonous embryos are known in *Cycadeoidea* (Crepet, 1974; Wieland, 1906, 1916).

#### GNETALES

A cladogram for the Gnetales has been presented already (Fig. 4). Only a general description of the Gnetales is given here as a basis for assessing their relationship with other seed plants.

The stelar morphology of *Gnetum* and *Welwitschia* is poorly known, but in *Ephedra* the primary vasculature is a eustele (Beck et al., 1982: 757–759). In *Ephedra* there is a single ring of vascular bundles with secondary xylem and phloem, but in *Gnetum* and *Welwitschia* there may be several concentric rings. The secondary xylem tissue consists of tracheids with circular bordered pits, vessels, and axial parenchyma. Axillary branching occurs in all genera, but leaf morphology is variable, ranging from the reticulate veined leaves of *Gnetum* to the strap-shaped parallel veined leaves of *Welwitschia*, and the scale-like or needle-like leaves of *Ephedra*.

The morphology and arrangement of the ovulate and microsporangiate reproductive structures of the Gnetales have been discussed already. The ovules generally are small, and the innermost layer of the various ovular coverings generally is regarded as a single integument. It is "fused" with the nucellus for about half its length. Apically the integument forms an elongated micropylar tube. The ovules of *Gnetum* and *Welwitschia* are not obviously flattened, although in *Welwitschia* there are a pair of minute lateral flaps at the base of the non-functional ovule in the microsporangiate flower. In some species of *Ephedra* (e.g., *E. distachya*) the integument originates from a pair of dorsiventral primordia (Martens, 1971, fig. 24.4, 24.5), and at maturity there are two integumentary vascular bundles (Eames, 1952: 87). In some species of *Ephedra*, therefore, the ovules appear to be platyspermic, but the orientation of the primary plane is at 90° to the bract unlike the situation occurring in conifers. The acid-resistant megaspore membrane of mature seeds in the Gnetales is either ex-



tremely thin (about 1  $\mu\text{m}$ ) as in *Welwitschia* and *Ephedra* or lacking altogether in *Gnetum* (Erdtman, 1965; Thomson, 1905).

The microsporangiate structures of *Welwitschia* and some species of *Ephedra* are arranged in a whorl, although in *Gnetum* the microsporangia are borne on a solid structure (character 1.7). Gnetalean pollen has already been described (character 1.5), and the evidence currently available (Van Campo & Lugardon, 1973) suggests that the exine is comprised of a tectum, a granular interstitium, and a thick, laminated inner layer. Microgametophyte development (character 1.1) and megagametophyte development (characters 1.2, 1.3) in the Gnetales have already been described. Embryogenesis varies in the three genera. In *Ephedra* there is a short free nuclear phase, but in *Welwitschia* embryogenesis is completely cellular. In *Gnetum* there are reports of both a free nuclear phase and completely cellular embryogenesis (Martens, 1971: 265).

#### ANGIOSPERMS

Most estimates place the total number of angiosperm species at around 250,000–300,000. This enormous number, coupled with extreme morphological diversity and inadequate comparative knowledge, makes the angiosperms extremely difficult to deal with as a group in a broad cladistic analysis such as this (Hill & Crane, 1982). Although it is widely accepted that the Magnoliidae and some monocotyledons have retained a relatively large number of primitive characters, they are still an extremely heterogeneous assemblage within which it is difficult to come to definite conclusions concerning likely plesiomorphic features. This difficulty is well illustrated by the argument over whether the angiosperms are primitively vesselless (Young, 1981). In the case of the few higher dicotyledons that lack vessels, this can be reasonably hypothesized as secondary loss, but in the case of vesselless magnoliid plants, this is much more problematic. The issue can only be resolved by a well corroborated phylogenetic analysis of relationships within the primitive angiosperms (Riggins & Farris, 1983). Until such a phylogenetic hypothesis is available for primitive flowering plants, the analysis provided here can only be regarded as preliminary. Characters of flowering plants are considered individually as part of the character discussion given below.

#### PHYLOGENETIC RELATIONSHIPS OF EXTANT AND FOSSIL GYMNOSPERMS

##### ANALYSIS OF CHARACTERS

**9.1 Eustele.** Beck et al. (1982: 701) define a eustele as “a stele with a hollow cylinder or tubular mass of tissue (i.e., with or without definable pith) and with discrete sympodia usually either as a discontinuous cylinder or in a scattered and dispersed arrangement.” This kind of stele occurs in *Archaeopteris* and most seed plants and contrasts with the protosteles or siphonosteles typical of pteridophytes, including the aneurophytalean progymnosperms (Beck et al., 1982: 726). Fossil taxa with unknown stem anatomy (peltasperms, *Caytonia*) are assumed for present purposes to have had a eustele. The angiosperms too are interpreted here as fundamentally eustelic although this has been disputed by Tomlinson (1984) particularly for the monocotyledons. A few seed plants, however, are protostelic, particularly among the “lyginopterid seed ferns” (e.g., *Heterangium*, *Micropermopteris*, *Tetrastichia*, Taylor, 1981a). Out-group comparison with all pteridophytes, except *Archaeopteris*, suggests that this may be the primitive condition for seed plants as a whole. On this basis *Quaestora* probably exhibits the primitive medullosan condition, the “polystelic” eustele having evolved *within* the group. The medullosans are therefore treated as protostelic in this analysis.

**9.2 Embryogenesis with a free nuclear phase.** In extant bryophytes and pteridophytes all of the divisions of the zygote following fertilization involve the formation of cell walls (Sporne, 1970). Embryogenesis is cellular throughout. In embryos of extant cycads and *Ginkgo* a coenocytic phase with 250 or more nuclei may be produced before cellularization occurs. In *Ephedra* and most conifers there is a short free nuclear phase of approximately three zygotic divisions. The presence of a free nuclear phase in embryogenesis is interpreted (Hill & Crane, 1982) as a specialized feature of seed plants by out-group comparison with pteridophytes. In *Welwitschia* and angiosperms (Martens, 1971: 265) embryogenesis is cellular throughout. In *Gnetum* whether early embryogenesis is cellular or has a free nuclear phase is uncertain (Martens, 1971: 265). The primitive condition is assumed in this analysis. A few conifers have wholly cellular embryogenesis (e.g., *Sequoia*, Martens, 1971: 265), but these taxa are specialized within the



conifer clade (Miller, 1982). I interpret this feature as a secondary advance within the group. As Chamberlain (1935: 342) suggested, there may be a correlation in seed plants between egg-cell size and the duration of the free nuclear phase. Embryogenesis for all fossil seed plants considered is unknown but is treated here as having involved a free nuclear phase. In *Archaeopteris*, however, in line with other presumed pteridophytic aspects of its reproductive biology (Pettitt, 1970), I have treated embryogenesis as being cellular throughout.

**9.3 Single functional megaspore mother-cell per megasporangium.** With the exception of *Archaeopteris* the megasporangium in all of the taxa considered here produces one functional megaspore mother-cell. In all seed plants except *Gnetum*, *Welwitschia*, and a few angiosperms (character 9.28) one functional megaspore is subsequently formed, and the remaining three megaspores abort. Under this interpretation the female gametophyte develops entirely within the megaspore, and the tissues of the megasporangium are regarded as homologous with the nucellus. In heterosporous species of *Archaeopteris* and most heterosporous pteridophytes (e.g., *Selaginella*) more than one megaspore is produced in each megasporangium. A few pteridophytes such as the extant fern *Marsilea*, the fossil lepidodendroid genera *Achlamydocarpon* and *Lepidocarpon*, the probable herbaceous Pennsylvanian lycopod *Miadesmia*, and the fossil sphenopsid *Calamocarpon* also have a single functional megaspore per megasporangium, but the distribution of other characters (not analyzed here) indicates that these are not homologous with the seed plant situation. This is the widely accepted view (Stewart, 1983).

**9.4 Integument.** All of the taxa considered in this analysis except *Archaeopteris* have the megasporangium (nucellus) surrounded by an integument. This feature has been given various interpretations in different groups of seed plants (see characters 9.7, 9.19), but no comparable structure occurs in extant pteridophytes. Enclosure of the megasporangium in the fossil lycopods *Lepidocarpon* and *Miadesmia* is achieved by lateral extensions of the megasporophyll that extend around the equator of the megaspore. This is not homologous with the situation in seed plants (Stewart, 1983) where enclosure has apparently occurred along the polar axis of the megaspore.

**9.5 Micropyle.** All seed plants considered in this study have a clearly defined micropyle, and

although the integument may have a pair of lateral "horns" (e.g., conifers, *Ginkgo*) or be elongated to form a long micropylar tube (e.g., corytosperms, Bennettitales, Gnetales), it is never deeply lobed around the micropyle as in early seed plants such as *Archaeosperma* (Pettitt & Beck, 1968; Pettitt, 1970). I interpret the unlobed micropyle as a derived feature that unites all the seed plants considered in this study (see also Stewart, 1983). *Archaeosperma*, the early seeds described by Gillespie et al. (1981), *Genomosperma kidstonii*, and *G. latens* (Long, 1959) all have a poorly differentiated micropyle that I interpret as the primitive condition. The lobed micropyle of some angiosperms (e.g., *Hernandia*) is clearly not homologous with the condition in early seed plants.

**9.6 Linear tetrad of megaspores.** Meiosis of the megaspore mother-cell in all extant seed plants produces a linear tetrad of megaspores of which only the inner develops, or female gametophyte development is tetrasporic (*Gnetum*, *Welwitschia*, and a few angiosperms, character 9.28). Most angiosperms produce a linear tetrad (Sporne, 1974: 162). In the fossil taxa considered in this study probable linear tetrads of megaspores have been described only in *Cycadeoidea* (Crepet, 1974; Crepet & Delevoryas, 1972), but the absence of haptotypic markings on the megaspores of all other taxa where this has been examined suggests that they also may have been produced in linear tetrads. Comparison of *Lyginopteris* with other "lyginopterid seed ferns" suggests that the megaspores may have developed from a tetrahedral tetrad. By out-group comparison with megaspores of pteridophytes and early seed plants (e.g., *Archaeosperma*, Chaloner & Pettitt, 1964; Pettitt, 1970) I interpret *Lagenostoma* (*Lyginopteris*) as primitive in this character.

**9.7 Double vascular supply to ovules.** Cycads and medullosans both have large ovules, which are supplied by a radially arranged double vascular system. The outer ring of bundles supplies the sarcotesta. In medullosans, the nucellus and integument are free except at the chalaza, and the inner ring of bundles supplies the nucellus; but in cycads where the nucellus is "fused" to the integument for most of its length, it is rarely clear whether the inner bundles are in nucellar or integumentary tissue. This double vascular supply to the ovules is not known to occur in any of the other taxa considered in this study.

Rodin and Kapil (1969) have compared the ovule vasculature of *Gnetum* with that of *Pachy-*



*testa*, but under the interpretation given here (character 9.33) only the inner envelope of a *Gnetum* ovule is a true integument, and therefore the two outer layers do not have homologues in cycads or medullosans. In *Lagenostoma* (*Lyginopteris*) there is a unitegmatic ovule with a radial vascular supply inside a vascularized cupule. It has been suggested (Sporne, 1971a: 61; Wordsell, 1906) that this cupule may be homologous with the integument of cycads and medullosans and that their inner vascular system represents the remains of an "inner" integument. However, the "inner" integument of *Lagenostoma* is differentiated into a sarcotesta, a sclerotesta, and endotesta as in most gymnosperm seeds, including those of cycads and medullosans. There is no evidence in cycads and medullosans, other than the vasculature, for an additional tissue layer in the integument, and the "double integument" interpretation is not accepted in this paper (see also Stewart, 1983). Similarly the pad of vascular tissue at the base of *Cardiocarpus* and *Mitrospermum* ovules is not taken to indicate the former presence of an "inner integument" (Graham, 1935). In peltasperms and corystosperms ovule vasculature is unknown but assumed not to have been double as in cycads and medullosans.

Only the inner integument of angiosperms is interpreted in this study as homologous to the integument of other seed plants (character 9.19). Very few angiosperms have a vascularized inner integument (Sporne, 1974: 154), and I know of none in which a double vascular system has been described.

**9.8 Axillary branching.** Despite intensive study of anatomically preserved material, axillary branching has not been reported in progymnosperms. Axillary branching has also never been demonstrated in extant cycads (p. 744). In all other plants considered in this study axillary branching is either known or is assumed (peltasperms, corystosperms) to have been present.

**9.9 Saccate pollen.** Saccate pollen or prepollen is generally regarded as the primitive condition in conifers and cordaites, but also occurs in *Callistophyton*, glossopterids, *Caytonia*, and corystosperms. Saccate pollen is interpreted as a relatively specialized feature within seed plants, although it should be noted that saccate spores occur in some aneurophytalean progymnosperms (e.g., *Rellimia*, *Tetraxylopteris*; Bonamo, 1977; Bonamo & Banks, 1967; Leclercq & Bonamo, 1971; Scheckler & Banks, 1971) and Penn-

sylvanian lycopods (Kosanke, 1969; Pigg & Rothwell, 1983). Saccate pollen reported in medullosans (*Parasporites* in *Parasporotheca* Dennis & Eggert, 1978) is treated here as specialized within that group.

**9.10 Flattened ovules.** Flattened ovules with one or two planes of symmetry occur in conifers, cordaites, *Callistophyton*, and all of the "Mesozoic seed ferns" (peltasperms, glossopterids, *Caytonia*, corystosperms, *Pentoxylon*). Flattened ovules also occur in some lyginopterid seed ferns (not *Lagenostoma*) that are too poorly known to evaluate their relationships further (e.g., *Lyrasperma*, Long, 1960). In cordaites, conifers, *Callistophyton*, *Caytonia*, and *Ephedra* there are two vascular bundles in the primary plane that run in the sarcotesta for most of their length, but in *Ginkgo* the bundles run within the endotesta. In the Bennettitales the ovules are small, with no integumentary vascular tissue, and are generally regarded as radiospermic. However, in the primitive bennettitalean genus *Vardekloeftia* (Figs. 9B, C, 12) and in the Upper Triassic *Bennetticarpus wettsteinii* (Kräusel, 1949), the ovules are relatively large (7–10 mm long) and flattened. More detailed examinations of the ovules in primitive Bennettitales are required, but here I interpret this platyspermy as primitive for the Bennettitales on the basis that the ovules resemble those of Mesozoic seed ferns, *Callistophyton*, cordaites, and other groups mentioned above. The integument of *Gnetum* ("endotesta" of Rodin & Kapil, 1969) has a well-developed radial vascular system; and *Welwitschia* ovules are unvascularized and radiospermic.

The bitegmatic ovules of many angiosperms are bilaterally symmetrical and anatropous. However, if the interpretations accepted in this paper are correct (character 9.19), then this is homologous to a flattened recurved "cupule" containing a single unitegmatic ovule. A comparable situation occurs in the corystosperms, and in this group the primary plane of the ovule is aligned in the same plane as the "cupule" stalk. Although many bitegmatic ovules of angiosperms could be flattened "cupules," each containing a flattened seed, there is no convincing evidence that the nucellus and inner integument of angiosperm ovules are fundamentally platyspermic.

**9.11 Megaphyllous leaves organized on a pinnate plan.** Megaphyllous pinnately organized leaves occur in all taxa considered except *Archaeopteris*, cordaites, conifers, *Ginkgo*, *Welwitschia*, and *Ephedra*. In these taxa leaf vena-



tion is either univeined, dichotomous and diverging, or dichotomous and basically parallel. Although reticulations do occur they are not well developed. In angiosperms the parallel or dichotomously veined leaves of *Kingdonia*, *Circaeaster*, and many monocotyledons (Foster & Gifford, 1974) are interpreted as secondary advances within the angiosperm clade. Megaphyllous leaves are not known to occur in progymnosperms.

**9.12 Narrowly triangular awl-shaped leaves.** This feature already has been discussed in relation to conifers (character 3.1). The triangular leaves in *Ephedra* and a few, presumably derived, angiosperms are only superficially like those of conifers, but in *Cordaixylon*, *Mesoxylon*, *Lyginopteris*, and *Callistophyton* scale-like leaves similar to those of conifers are occasionally produced on proximal parts of branches and associated with axillary buds (Rothwell, 1982a). These heteroblastic leaf series may be important in the origin of conifer foliage (Rothwell, 1982a), but in this analysis the *consistent* production of narrowly triangular awl-shaped leaves only occurs in *Lebachia* and extant conifers.

**9.13 Megasporophylls borne on short fertile shoots in the axil of a bract or leaf.** This feature already has been discussed in relation to conifers (character 3.3). The megasporophylls of conifers, cordaites, and *Ginkgo* are all borne on fertile shoots in the axil of a bract or leaf. In the Gnetales the ovules are terminal. In peltasperms, *Caytonia*, and corystosperms it is not known how the megasporophylls were attached to the plant, but from their morphology it is unlikely that they were borne in a manner homologous with that of cordaites and conifers, and the unspecialized condition is assumed. In glossopterids (character 4.2) the megasporophylls were adnate to a subtending leaf or bract, but the morphological situation and homologies are unclear.

The interpretation of this character in flowering plants is dependent on whether the angiosperm carpel is regarded as a modified simple megasporophyll (e.g., Doyle, 1978) or a compound structure formed from a fertile branch in the axil of a subtending leaf or bract (e.g., Stebbins, 1974). This paper adopts the former interpretation (character 9.34). In some angiosperms (e.g., "Amentiferae," Chloranthaceae) the carpels are borne in the axil of a bract or leaf, but this is generally regarded as a secondary advance within the angiosperm clade (Walker & Walker, 1984).

**9.14 Fertile axillary ovulate shoots aggregated into an "inflorescence."** The fertile axillary ovulate shoots of cordaites and conifers are aggregated into an "inflorescence," but in *Ginkgo* the fertile axillary shoot is single in the axil of a leaf. The situation in cordaites and conifers is not known to occur in other seed plants considered in this study. The relationships of the enigmatic Southern Hemisphere conifers *Buriadia* and *Walkomiella*, and the possibility that they represent "the coneless ancestors of *Lebachia*-like conifers" (Pant, 1977b: 31) is not examined in this paper, although it is of interest to note that they may post-date *Lebachia* in the fossil record (Rothwell, 1982a; Pant, 1977b).

**9.15 Pollen with distal germinal aperture.** Pollen with a distal aperture (and therefore, presumably, distal germination) occurs in all of the seed plants considered here, with the exception of medullosans, *Lyginopteris*, and *Mesoxylon*, where the aperture is proximal (pre-pollen; Schopf, 1938; Chaloner, 1970a). Out-group comparison with pteridophytes suggests that distal germination is a derived feature. The pollen of *Lebachia* (*Potonieisporites*) has a proximal monolet suture but also frequently has two curved folds in the exine of the distal surface (Scott & Chaloner, 1983). However, material described by Mapes and Rothwell (1984) suggests that germination in *Potonieisporites* was proximal. In the Gnetales the distal aperture of *Welwitschia* is accepted as the primitive condition in the group relative to the inaperturate grains of *Ephedra* and *Gnetum* (character 1.5).

Although a few angiosperms have a proximal germinal aperture (Walker, 1974b), distal germination is widely considered to be primitive in the group (Chaloner, 1970a; Doyle, 1978; Walker, 1974b), equatorial germination being a subsequent development within the clade (Doyle, 1978).

**9.16 Cordaites foliage.** The characteristically strap-shaped foliage of *Cordaites* is known attached to *Cordaixylon dumusum* (Rothwell & Warner, 1984) and *Mesoxylon priapi* (Trivett & Rothwell, 1985). The leaves have dichotomous, more or less parallel veins and a characteristic internal anatomy with well-developed longitudinal fibrous ribs (Harms & Leisman, 1961). The leaves of *Welwitschia* are superficially similar but grow continuously from a basal meristem, and have much less well-developed sclerotic tissue (Martens, 1971: 94).

**9.17 Primary axis of ovulate and microspo-**



*rangiate "inflorescences" dorsiventrally flattened with bracts and fertile shoots four-ranked.* This character occurs only in *Cordaixylon* and *Mesoxylon* among the taxa studied.

**9.18 Siphonogamy.** Zooidogamy occurs in extant cycads and *Ginkgo*. All spores of living plants with proximal germination produce motile gametes (bryophytes, pteridophytes). This is the basis for inferring zooidogamy in those fossil taxa with proximal germinal apertures in their pollen (medullosans, *Lyginopteris*, *Mesoxylon*, *Lebachia*). *Callistophyton* is known to have produced a distal pollen tube, which was probably involved in gamete transfer. In this analysis all other fossil plants with distal germinal apertures in the pollen are scored uniformly as plesiomorphic in this feature.

**9.19 Ovules borne in a "cupule."** The ovules of glossopterids, *Caytonia*, and corystosperms are enclosed or partly enclosed by the megasporophyll lamina to form a "cupule." These Permian and Mesozoic "cupules" have frequently been compared, or considered homologous, to the cupules of Upper Devonian, Mississippian and Pennsylvanian seed ferns, such as *Archaeosperma* and *Lyginopteris* (Thomas, 1933, 1955; Townrow, 1960). Morphologically, however, there are at least two different kinds of structure. The cupules of *Lyginopteris* and other early pteridosperms are axially organized with respect to the long axis of the ovules they enclose. The stalk is axially attached and the construction of the cupule may reflect an origin either from sterile axes ("telomes") or the ultimate segments of a deeply divided leaf (e.g., *Archaeopteris*). In glossopterids, *Caytonia*, and corystosperms, the stalk of the cupule is lateral with respect to the long axis of the enclosed ovules. This lateral arrangement is most easily interpreted as reflecting an origin from modified pinnae or pinnules, such as those of *Autunia*, which have become rolled or expanded in various ways to form "cupular" pouches. Doyle (1978: 383) expressed a similar view that the "cupules" of Permian and Mesozoic seed ferns are more easily explained as "leaflets modified by various degrees of circinnate enrollment than as direct homologues of the bell-shaped cupules of lyginopterids."

According to the interpretation of "cupules" in *Caytonia*, corystosperms, and *Glossopteris* given above, the bitegmic ovule of angiosperms may be interpreted as a uniovulate "cupule." The idea that the outer integument in a bitegmic angiosperm ovule is homologous to the "cupule"

of "Mesozoic seed ferns" has been advocated by numerous authors (Doyle, 1978; Stebbins, 1974; Stewart, 1983). This view is supported by the recurved "anatropous" arrangement of the "cupule" in *Caytonia* and corystosperms, the zigzag micropyle of many bitegmic angiosperm ovules, and evidence that the funicle, chalaza, and outer integument are part of a single developmental unit (Bor, 1978), while the inner integument and nucellus are part of another. The complex net-like vasculature of the outer integument of many angiosperm ovules is a further similarity with the "cupules" of "Mesozoic seed ferns." The homology of the "cupules" of *Caytonia* and corystosperms with angiosperms is accepted in this paper as providing the most straightforward explanation of the second integument that does not require a de novo origin (cf. Long, 1966). Unitegmic ovules occur in relatively specialized flowering plants and are interpreted as a secondary development within the angiosperm clade.

In *Pentoxylon* and Bennettitales the homologies of the outer integument are more difficult to determine. In *Vardekloeftia* and *Bennetticarpus crossospermus* (Bennettitales) there is a distinct outer layer around the inner integument, which has been variously termed the "cupule" or "micropylar plate" (Harris, 1932b) and is interpreted here as the outer integument of a bitegmic ovule. In *Vardekloeftia* two seeds occasionally occur within a single "cupule," and this may indicate derivation from a structure that formerly contained more than one ovule (Harris, 1932b: 108). In *Cycadeoidea* Wieland (1906: 120) has described a "cup-shaped supporting basal husk," and in *Bennettites albianus* Stopes (1918) has described a "cupule or aril of elongated tubular cells." I suggest that both of these layers are homologous with the "cupule" of *Vardekloeftia* and *Bennetticarpus crossospermus* and the outer layer of *Bennetticarpus wettsteinii* seeds (Kräusel, 1949). In *Pentoxylon* I interpret the bennettitalean "cupule" as represented by the well-developed outer fleshy "sarcotesta" around each ovule, and the cuticle obtained from this layer in *Pentoxylon cranwellii* has been compared with that of the "cupule" in *Vardekloeftia* (Harris, 1962: 24).

On the interpretations of "cupules" given above the outer integument in the ovules of Bennettitales and *Pentoxylon* may be interpreted in three different ways. Either it is homologous with the cupule of *Lagenostoma* (*Lyginopteris*), or ho-



mologous with the “cupule” of glossopterids, *Caytonia*, corystosperms, and angiosperms, or it is independently derived and not homologous to either. In this paper I exclude the first possibility. Although the ovules of Bennettitales, *Pentoxylon*, and *Lagenostoma* are all orthotropous, they differ considerably in other features. The cupule of *Lagenostoma* is lobed, heavily vascularized, does not enclose the ovule, and is thought to have been borne on well-developed megaphylls. “Cupules” of primitive Bennettitales and *Pentoxylon* are unlobed, unvascularized, enclose the ovule, and are not borne on megaphylls.

The two remaining possibilities are considered by two different methods of scoring in the data matrix for this paper. In one analysis (cladogram 1, p. 770), the bennettitalean and *Pentoxylon* ovule is interpreted as non-homologous with the “cupules” of glossopterids, *Caytonia*, and corystosperms. In the second analysis (cladogram 2, p. 770) the homology of these different “cupules” (but not the cupule of the *Lyginopteris* plant) is accepted. The details of adjusting the data matrix for these two different interpretations are discussed later in the paper (p. 774).

In the Gnetales the only morphological features that may be interpreted as evidence for the presence of a “cupule” are the regular development of two nucelli within a single integument in some species of *Ephedra* (Thoday & Berridge, 1912), the two lateral flaps of tissue at the base of the non-functional ovule in microsporangiate “flowers” of *Welwitschia*, and the occasional occurrence of *Gnetum* ovules with four “integuments” (Pearson, 1915). In the absence of better evidence the Gnetales are treated as lacking a “cupule” in this analysis.

**9.20 Megaspore membrane thin.** Comparative information on the megaspore membranes of gymnosperms is inadequate. Currently available data suggest that a thick, well-developed acid-resistant megaspore membrane, like that typical of pteridophytes, is primitive within seed plants (Hill & Crane, 1982) and that the weakly developed membrane in *Caytonia*, corystosperms, *Pentoxylon*, Bennettitales, and angiosperms is a specialized condition (Erdtman, 1957, 1965; Harris, 1954; Thomson, 1905). The megaspore membrane in these plants is only weakly resistant to maceration, and frequently this seems to be correlated with the presence of a well-developed nucellar cuticle (Harris, 1954). In conifers the megaspore membrane varies in thickness between genera. A thin megaspore

membrane, however, is most common in relatively advanced taxa (Erdtman, 1965; Miller, 1982). In angiosperms the megaspore membrane can be detected with transmission electron microscopy (Mogensen, 1978) but is not acid-resistant.

**9.21 Granular pollen wall.** The pollen of all the seed plants considered here has two well-defined wall layers, the outer of which is either alveolar or granular in construction (Doyle et al., 1975). Within the alveolar forms there are two basic types; one in which the alveolae are comprised of small, typically densely crowded cavities (“cycad type,” Doyle et al., 1975), the other in which the alveolae are larger and more highly organized (“pinaceous type,” Doyle et al., 1975). The microspores of *Archaeopteris* (Pettitt, 1966) and the pollen of corystosperms, Bennettitales, and Gnetales all have a granular wall structure. Pollen of cycads and medullosans is of the alveolate type, with small cavities, and the pollen of conifers, cordaites, *Ginkgo*, *Callistophyton*, peltasperms, glossopterids, and *Caytonia* is of the more highly differentiated alveolate type (Crepet & Zavada, pers. comm.; Doyle et al., 1975; Millay & Taylor, 1976). Pollen of *Lyginopteris* has not been studied with transmission electron microscopy but is assumed to have had a homogeneous wall as in the pollen of *Crossotheca*. Pollen of *Pentoxylon* is currently under investigation (Taylor & Crane, in progress). Preliminary results from transmission electron microscopy suggest that the pollen wall is granular.

Granular pollen wall stratification occurs in many angiosperm groups, and in most cases (e.g., Juglandaceae, Betulaceae) it is interpreted as a secondary modification within flowering plants. However, granular exines also occur in many magnoliid families (e.g., Amborellaceae, Annonaceae, Canellaceae, Magnoliaceae) (Walker, 1976). Walker (1976: 278) suggests that these granular exines represent a stage in the origin of tectate wall structure from a homogeneous, walled, atectate primitive condition. However, in the gymnosperms studied in this analysis a homogeneous exine occurs only in *Lyginopteris*, and the basic pollen wall type appears to be the alveolar condition with granular exines a relatively specialized feature seen in corystosperms, Bennettitales, Gnetales, and, presumably as a secondary advance, in some conifers (e.g., Araucariaceae, Taxodiaceae). In the context of seed plants as a whole, I accept the hypothesis that



granular pollen wall stratification is primitive within angiosperms (see also Doyle, 1978: 375–376).

9.22 *Uniovulate "cupule."* The "cupules" of *Caytonia* and the glossopterids considered here contain several ovules. In the glossopterid *Denkania* (Pant, 1977a; Surange & Chandra, 1975) the "cupules" apparently contain a single ovule, but this is interpreted as a specialized feature within the glossopterid clade. According to the interpretation of character 9.19, the corystosperms, Bennettitales, *Pentoxylon*, and angiosperms also have a single ovule per "cupule." The homologies of "cupules" in all of these taxa are treated in two different ways (p. 770) but are not considered homologous with the cupules of *Lyginopteris* and other early seed ferns, for reasons given earlier (character 9.19).

9.23 *Microsporophylls forming "flowers."* The microsporophylls of the Bennettitales, *Pentoxylon*, *Ephedra*, and *Welwitschia* are aggregated together in a whorl or pseudowhorl to form cup-like "flowers" quite distinct from the pollen cones of conifers. In Bennettitales, *Welwitschia*, *Ephedra*, and angiosperms they are clearly arranged in a whorl or tight helix (see also character 9.33). The microsporophylls are similarly aggregated in *Pentoxylon* but details of their arrangement are uncertain. It is not known how the microsporophylls of corystosperms, *Caytonia*, glossopterids, and *Peltaspermum* were arranged on the plant, but in this analysis I have assumed that they were not aggregated into "flowers" (plesiomorphic condition).

9.24 *Uniovulate "cupule" erect.* The uniovulate "cupules" of corystosperms like the multiovulate "cupules" of *Caytonia* were recurved, and I interpret this as the primitive condition (see character 9.19). In Bennettitales and *Pentoxylon* the uniovulate "cupules" are borne erect. In flowering plants the most widespread, and apparently primitive, configuration for the bitegmic ovule is anatropous. This is consistent with derivation of the outer integument from a recurved *Caytonia*-like or corystosperm "cupule." Although orthotropous bitegmic ovules do occur, these are considered as specializations within the flowering plant clade.

9.25 *Megasporophylls "unicupulate."* In the Bennettitales and *Pentoxylon* the presumed homologues of the megasporophylls consist of a single "cupule" (character 9.19). In other Permian and Mesozoic plants with "cupules" (*Caytonia* and corystosperms) there are several "cu-

pules" per megasporophyll, and in *Glossopteris* this is also interpreted as the primitive condition (character 4.5).

In angiosperms the primitive carpel appears to be conduplicate, containing several seeds (Bailey & Swamy, 1951). Under the interpretation adopted in this paper, each carpel would therefore consist of several cupules, perhaps originating in the manner suggested by Doyle (1978). Although some of the carpels in the Magnoliidae (e.g., Chloranthaceae) contain only a single ovule, they are interpreted here as a secondary modification within flowering plants (Walker & Walker, 1984).

9.26 *"Unicupulate" megasporophylls aggregated to form heads.* In *Pentoxylon* and Bennettitales the "unicupulate" megasporophylls (characters 9.19, 9.25) are aggregated together to form heads. No comparable arrangement occurs in any other seed plant considered in this analysis.

9.27 *Male gametophyte of three or four nuclei.* In gymnosperms, a male gametophyte of four nuclei occurs only in *Gnetum*, *Welwitschia*, and some conifers (character 1.1). In angiosperms the male gametophyte is even less extensive and undergoes two mitotic divisions to produce three cells.

9.28 *Female gametophyte tetrasporic.* In *Gnetum* and *Welwitschia* (character 1.2), the female gametophyte is tetrasporic. Tetrasporic megagametophytes are uncommon in angiosperms (Sporne, 1974: 162) and are interpreted as a secondary development within the flowering plant clade.

9.29 *Archegonia absent.* As in *Gnetum* and *Welwitschia* (character 1.3), no archegonia are differentiated in the female gametophyte of angiosperms. However, the megagametophytes in these two groups differ markedly in both development and mature structure. For these reasons they are not accepted a priori as homologous in this analysis.

9.30 *Embryo with "feeder."* There is no structure comparable to the "feeder" of *Gnetum* and *Welwitschia* (character 1.4) in the embryo of angiosperms or any other seed plant.

9.31 *Ribbed pollen.* Ribbed pollen superficially similar to that of *Ephedra* and *Welwitschia* (character 1.5) occurs in some angiosperms (e.g., *Spathiphyllum*, Araceae; Trevisan, 1980). However, transmission electron microscopy shows that the ribs in *Spathiphyllum* are formed by a tectate columellate wall rather than by granular



exine as in *Ephedra* and *Welwitschia* (Trevisan, 1980). Ribbed pollen known to occur in Acanthaceae is also interpreted as a secondary development within the angiosperm clade.

**9.32 Vessels with porose perforation plates.** Vessels occur in the Gnetales (character 1.6) and most angiosperms. Although they have also been reported in the Bennettiales (Krassilov, 1984) they are not known to be general within that group. Typically the vessels of Gnetales and angiosperms have been regarded as independently derived from tracheids, with circular bordered pits and scalariform pitting, respectively (Cronquist, 1968). It also has been generally accepted that vessels arose *within* the angiosperms and that magnoliid angiosperms that lack vessels are primitively vesselless. However, Young (1981) has recently questioned whether the angiosperms are primitively vesselless. His analysis of relationships within the Magnoliidae suggests that it is more parsimonious to invoke loss of vessels rather than the multiple vessel origins, but this should not be taken to imply that angiosperm and gnetalean vessels are necessarily homologous. Muhammad and Sattler (1982), however, have described "scalariform" and "scleroid" perforation plates in *Gnetum*, which further blur the distinctions between angiosperm and gnetalean vessels.

Despite these difficulties the traditional view, that vessels of Gnetales and angiosperms are non-homologous, is adopted in this paper. A more detailed evaluation of relationships within the Magnoliidae is required to evaluate the systematic position of vesselless taxa. Also, the similarities in perforation plates, of *Gnetum* and angiosperms described by Muhammad and Sattler (1982), involve taxa that are regarded as relatively derived within flowering plants (e.g., various "Amentiferae").

**9.33 Microsporangiate and ovulate "flowers" with opposite pairs of bracteoles.** The reproductive structures of the Gnetales and several angiosperm groups are arranged on an opposite and decussate plan (character 1.7). In many cases, such as the "Amentiferae," this arrangement is thought to be a secondary modification within the flowering plant clade. This probably also is the case in more primitive angiosperms such as Chloranthaceae (Walker & Walker, 1984, fig. 111).

**9.34 Bitegmic ovule enclosed or partially enclosed by a structure with a pollen-receptive stigmatic surface external to the second integu-**

**ment.** Several living and extinct gymnosperms show total or partial enclosure of a unitegmic ovule (e.g., *Caytonia*, corystosperms, Bennettiales, glossopterids, and some conifers), and some (e.g., *Tsuga* and perhaps *Leptostrobus*) have a pollen-receptive surface external to the micropyle. However, no known gymnosperm has an enclosed, or partially enclosed, bitegmic ovule and a pollen-receptive stigmatic surface external to the outer integument. It is assumed here that those angiosperms with unitegmic ovules represent a secondary modification within the flowering plant clade.

Numerous mechanisms have been suggested for the enclosure of angiosperm ovules and the formation of a simple conduplicate carpel. In this paper the hypothesis is adopted that the carpel represents a "cupulate" megasporophyll such as occurs in *Caytonia* and corystosperms, perhaps modified by progenesis (Doyle, 1978).

**9.35 Female gametophyte of 4–16 nuclei.** In all seed plants where it is known, the female gametophyte is much more extensive than in angiosperms.

**9.36 Double fertilization.** The process of double fertilization in angiosperms that results in the formation of a zygote and endosperm nucleus does not occur in other seed plants. The closest approach to the angiosperm situation is in *Ephedra*, in which one of the male gametes fuses with the ventral canal nucleus of the archegonium, but this second zygote undergoes no further divisions (Moussel, 1978; Sporne, 1971a: 187).

**9.37 Laminate endexine lacking.** All gymnosperm pollen that has been studied in sufficient detail has a laminate endexine. In angiosperms the endexine is generally unlaminated except close to the apertures (Doyle et al., 1975), and some angiosperms appear to lack any endexinous layer (Walker, 1974a). Lugardon and LeThomas (1974) have suggested that the laminated endexine of gymnosperms is in fact homologous to the foot layer (innermost ectexine) of angiosperm pollen and that the endexine of angiosperms arose *de novo* (Zavada, 1984). If this interpretation is accepted, then the apparent endexinous laminations of some Annonaceae (Walker, 1976) and Trimeniaceae (Sampson & Endress, 1984) are not homologous to those of gymnosperms. Interpreting this complex character is difficult (Hill & Crane, 1982: 344–345) and requires further investigation aimed particularly at clarifying general patterns of pollen wall ontogeny.



TABLE 9. Data matrix for characters of seed plants: apomorphic characters marked +, plesiomorphic characters marked −, not applicable marked NA. Cladogram 1 (Fig. 20) was constructed from version one of the data in which Bennettitales and *Pentoxylon* were scored as plesiomorphic for characters 9.19 and 9.22; and character 9.25 was excluded as redundant. Cladogram 2 (Fig. 22) was constructed from version two of the data in which Bennettitales and *Pentoxylon* were scored apomorphic for characters 9.19, 9.22, and 9.25. See text for further discussion of these two alternatives.

| Character                                                                                                                                 | <i>Archae-<br/>opteris</i> | Medul-<br>losans | Cycads | <i>Lygin-<br/>opte-<br/>ris</i> | <i>Cor-<br/>daixy-<br/>lon</i> | <i>Mes-<br/>oxylon</i> | <i>Le-<br/>bach-<br/>ia</i> | Ex-<br>tant<br>Coni-<br>fers |
|-------------------------------------------------------------------------------------------------------------------------------------------|----------------------------|------------------|--------|---------------------------------|--------------------------------|------------------------|-----------------------------|------------------------------|
| 1. Eustele                                                                                                                                | +                          | −                | +      | +                               | +                              | +                      | +                           | +                            |
| 2. Embryogenesis with a free nuclear phase                                                                                                | −?                         | +?               | +      | +?                              | +?                             | +?                     | +?                          | +                            |
| 3. Single functional megaspore mother-cell per megasporangium                                                                             | −                          | +                | +      | +                               | +                              | +                      | +                           | +                            |
| 4. Integument                                                                                                                             | −                          | +                | +      | +                               | +                              | +                      | +                           | +                            |
| 5. Micropyle                                                                                                                              | NA                         | +                | +      | +                               | +                              | +                      | +                           | +                            |
| 6. Linear tetrad of megaspores                                                                                                            | −                          | +?               | +      | −                               | +?                             | +?                     | +?                          | +                            |
| 7. Double vascular supply to ovules                                                                                                       | NA                         | +                | +      | −                               | −                              | −                      | −                           | −                            |
| 8. Axillary branching                                                                                                                     | −                          | +                | −      | +                               | +                              | +                      | +                           | +                            |
| 9. Saccate pollen                                                                                                                         | NA                         | −                | −      | −                               | +                              | +                      | +                           | +                            |
| 10. Flattened ovules                                                                                                                      | NA                         | −                | −      | −                               | +                              | +                      | +                           | +                            |
| 11. Megaphyllous leaves organized on a pinnate plan                                                                                       | −                          | +                | +      | +                               | −                              | −                      | −                           | −                            |
| 12. Narrowly triangular awl-shaped leaves                                                                                                 | −                          | −                | −      | −                               | −                              | −                      | +                           | +                            |
| 13. Megasporophylls borne on short fertile shoots in the axil of a bract or leaf                                                          | −                          | −                | −      | −                               | +                              | +                      | +                           | +                            |
| 14. Fertile axillary ovulate shoots aggregated into an “inflorescence”                                                                    | NA                         | NA               | NA     | NA                              | +                              | +                      | +                           | +                            |
| 15. Pollen with distal germinal aperture                                                                                                  | −                          | −                | +      | −                               | +                              | −                      | −                           | +                            |
| 16. <i>Cordaite</i> foliage                                                                                                               | −                          | −                | −      | −                               | +                              | +                      | −                           | −                            |
| 17. Primary axis of ovulate and microsporangiate “inflorescences” dorsiventrally flattened with bracts and fertile shoots four-ranked     | NA                         | NA               | NA     | NA                              | +                              | +                      | −                           | −                            |
| 18. Siphonogamy                                                                                                                           | NA                         | −?               | −      | −?                              | −?                             | −?                     | −?                          | +                            |
| 19. Ovules borne in a “cupule”                                                                                                            | NA                         | −                | −      | −                               | −                              | −                      | −                           | −                            |
| 20. Megaspore membrane thin                                                                                                               | −                          | −                | −      | −                               | −                              | −                      | −                           | −                            |
| 21. Granular pollen wall                                                                                                                  | +                          | −                | −      | +?                              | −                              | −                      | −                           | −                            |
| 22. Uniovulate “cupule”                                                                                                                   | NA                         | NA               | NA     | NA                              | NA                             | NA                     | NA                          | NA                           |
| 23. Microsporophylls forming “flowers”                                                                                                    | −                          | −                | −      | −                               | −                              | −                      | −                           | −                            |
| 24. Uniovulate “cupule” erect                                                                                                             | NA                         | NA               | NA     | NA                              | NA                             | NA                     | NA                          | NA                           |
| 25. Megasporophylls “unicupulate”                                                                                                         | NA                         | NA               | NA     | −                               | NA                             | NA                     | NA                          | NA                           |
| 26. “Unicupulate” megasporophylls aggregated to form heads                                                                                | NA                         | NA               | NA     | NA                              | NA                             | NA                     | NA                          | NA                           |
| 27. Male gametophyte of three or four nuclei                                                                                              | −?                         | −?               | −      | −?                              | −                              | −                      | −?                          | −                            |
| 28. Female gametophyte tetrasporic                                                                                                        | −                          | −?               | −      | −?                              | −?                             | −?                     | −?                          | −                            |
| 29. Archegonia absent                                                                                                                     | −?                         | −                | −      | −                               | −                              | −?                     | −?                          | −                            |
| 30. Embryo with “feeder”                                                                                                                  | −?                         | −?               | −      | −?                              | −?                             | −?                     | −?                          | −?                           |
| 31. Ribbed pollen                                                                                                                         | −                          | −                | −      | −                               | −                              | −                      | −                           | −                            |
| 32. Vessels with porose perforation plates                                                                                                | −                          | −                | −      | −                               | −                              | −                      | −                           | −                            |
| 33. Microsporangiate and ovulate “flowers” with opposite pairs of bracteoles                                                              | NA                         | NA               | NA     | NA                              | NA                             | NA                     | NA                          | NA                           |
| 34. Bitegmic ovule enclosed or partly enclosed by a structure with a pollen-receptive stigmatic surface external to the second integument | NA                         | NA               | NA     | NA                              | NA                             | NA                     | NA                          | NA                           |



TABLE 9. Continued.

| <i>Ginkgo</i> | <i>Cal-<br/>listo-<br/>phyton</i> | <i>Pelta-<br/>sperms</i> | <i>Glos-<br/>sopter-<br/>ids</i> | <i>Cay-<br/>tonia</i> | <i>Co-<br/>rysto-<br/>sperms</i> | <i>Bennet-<br/>tiales</i> | <i>Pent-<br/>oxylon</i> | <i>Gnetum</i> | <i>Wel-<br/>witschia</i> | <i>Ephed-<br/>ra</i> | <i>Angio-<br/>sperms</i> |
|---------------|-----------------------------------|--------------------------|----------------------------------|-----------------------|----------------------------------|---------------------------|-------------------------|---------------|--------------------------|----------------------|--------------------------|
| +             | +                                 | +?                       | +                                | +?                    | +                                | +                         | +                       | +             | +                        | +                    | +                        |
| +             | +?                                | +?                       | +?                               | +?                    | +?                               | +?                        | +?                      | +             | —                        | +                    | —                        |
| +             | +                                 | +                        | +                                | +                     | +                                | +                         | +                       | +             | +                        | +                    | +                        |
| +             | +                                 | +                        | +                                | +                     | +                                | +                         | +                       | +             | +                        | +                    | +                        |
| +             | +                                 | +                        | +                                | +                     | +                                | +                         | +                       | +             | +                        | +                    | +                        |
| +             | +?                                | +?                       | +?                               | +?                    | +?                               | +                         | +?                      | NA            | NA                       | +                    | +                        |
| —             | —                                 | —?                       | —                                | —                     | —?                               | —                         | —                       | —             | —                        | —                    | —                        |
| +             | +                                 | +?                       | +                                | +                     | +?                               | +                         | +                       | +             | +                        | +                    | +                        |
| —             | +                                 | —                        | +                                | +                     | +                                | —                         | —                       | —             | —                        | —                    | —                        |
| +             | +                                 | +                        | +                                | +                     | +                                | +                         | +                       | —             | —                        | +                    | —                        |
| —             | +                                 | +                        | +                                | +                     | +                                | +                         | +                       | +             | —                        | —                    | +                        |
| —             | —                                 | —                        | —                                | —                     | —                                | —                         | —                       | —             | —                        | —                    | —                        |
| +             | —                                 | —?                       | —?                               | —?                    | —?                               | —                         | —                       | —             | —                        | —                    | —                        |
| NA            | NA                                | NA?                      | NA?                              | NA?                   | NA?                              | NA                        | NA                      | NA            | NA                       | NA                   | NA                       |
| +             | +                                 | +                        | +                                | +                     | +                                | +                         | +                       | +             | +                        | +                    | +                        |
| —             | —                                 | —                        | —                                | —                     | —                                | —                         | —                       | —             | —                        | —                    | —                        |
| NA            | NA                                | NA?                      | NA?                              | NA?                   | NA?                              | NA                        | NA                      | —             | —                        | —                    | NA                       |
| —             | +                                 | —?                       | —?                               | —?                    | —?                               | —?                        | —?                      | +             | +                        | +                    | +                        |
| —             | —                                 | —                        | +                                | +                     | +                                | —/+                       | —/+                     | —             | —                        | —                    | +                        |
| —             | —                                 | —                        | —                                | +                     | +                                | +                         | +                       | +             | +                        | +                    | +                        |
| —             | —                                 | —                        | —                                | —                     | +                                | +                         | +                       | +             | +                        | +                    | +                        |
| NA            | NA                                | NA                       | —                                | —                     | +                                | —/+                       | —/+                     | NA            | NA                       | NA                   | +                        |
| —             | —                                 | —?                       | —?                               | —?                    | —?                               | +                         | +                       | —             | +                        | +                    | +                        |
| NA            | NA                                | —                        | —                                | —                     | —                                | +                         | +                       | NA            | NA                       | NA                   | —                        |
| NA            | NA                                | —                        | —                                | —                     | —                                | —/+                       | —/+                     | NA            | NA                       | NA                   | —                        |
| NA            | NA                                | NA                       | NA                               | NA                    | NA                               | +                         | +                       | NA            | NA                       | NA                   | NA                       |
| —             | —                                 | —?                       | —?                               | —?                    | —?                               | —?                        | —?                      | +             | +                        | —                    | +                        |
| —             | —?                                | —?                       | —?                               | —?                    | —?                               | —                         | —?                      | +             | +                        | —                    | —                        |
| —             | —                                 | —?                       | —                                | —?                    | —?                               | —?                        | —?                      | +             | +                        | —                    | —                        |
| —             | —                                 | —?                       | —?                               | —?                    | —?                               | —                         | —?                      | +             | +                        | —                    | —                        |
| —             | —                                 | —                        | —                                | —                     | —                                | —                         | —                       | —             | +                        | +                    | —                        |
| —             | —                                 | —?                       | —                                | —?                    | —                                | —                         | —                       | +             | +                        | +                    | —                        |
| NA            | NA                                | NA?                      | NA?                              | NA?                   | NA?                              | —                         | —                       | +             | +                        | +                    | —                        |
| NA            | NA                                | NA                       | NA                               | NA                    | —                                | —                         | —                       | NA            | NA                       | NA                   | +                        |



TABLE 9. Continued.

| Character                                                                                                    | <i>Archaeopteris</i> | Medullosans | Cycads | <i>Lyginopteris</i> | <i>Cor-daixylon</i> | <i>Mes-oxylon</i> | <i>Le-bachia</i> | Ex-tant Conifers |
|--------------------------------------------------------------------------------------------------------------|----------------------|-------------|--------|---------------------|---------------------|-------------------|------------------|------------------|
| 35. Female gametophyte of four to 16 nuclei                                                                  | –?                   | –           | –      | –                   | –                   | –?                | –?               | –                |
| 36. Double fertilization                                                                                     | –?                   | –?          | –      | –?                  | –?                  | –?                | –?               | –                |
| 37. Laminate endexine lacking                                                                                | –?                   | –           | –      | –?                  | –?                  | –?                | –?               | –                |
| 38. Axially aligned companion cells derived ontogenetically from the same mother-cells as the sieve elements | –?                   | –?          | –      | –?                  | –?                  | –?                | –?               | –                |

9.38 *Axially aligned companion cells derived ontogenetically from the same mother-cells as the sieve elements.* This character apparently occurs only in angiosperms and is not known in any other group of seed plants (Hill & Crane, 1982).

CLADOGRAMS

Cladograms were generated from the data matrix using the PAUP Program (Phylogenetic Analysis Using Parsimony) of D. L. Swofford with the global branch swapping and MULPARS option. Cladograms were rooted by incorporation of a hypothetical ancestor scored as plesiomorphic for all characters. Two different forms of the matrix (Table 9) were used to generate two different cladograms as follows.

*Cladogram 1* (Fig. 20). Cladogram 1 was generated from version one of the data matrix in which the “cupules” of Bennettitales and *Pentoxylon* were not coded as homologous to the “cupules” of glossopterids, *Caytonia*, corystosperms, and angiosperms. That is, Bennettitales and *Pentoxylon* were coded as plesiomorphic for characters 9.19 and 9.22. Character 9.25 was excluded as redundant (coded by character 9.24) giving in a total of 37 characters. The analysis resulted in five equally parsimonious cladograms (61 character state transitions) all with very similar topologies. A strict consensus tree (Rohlf, 1982) derived from those five cladograms is given in Figure 20. This kind of consensus tree preserves only those aspects of tree topology that occur in the five original trees. In this case the consensus tree only resulted in one polychotomy.

*Cladogram 2* (Fig. 22). Cladogram 2 was generated from version two of the data matrix in which the “cupules” of Bennettitales were coded as homologous to those of glossopterids, *Caytonia*, corystosperms, and angiosperms. That is,

Bennettitales and *Pentoxylon* were coded as apomorphic for characters 9.19, 9.22, 9.24, 9.25, giving a total of 38 characters. The analysis resulted in ten equally parsimonious cladograms (62 character state transitions) all with very similar topologies. A strict consensus tree derived from these ten cladograms is given in Figure 22.

DISCUSSION AND INTERPRETATION  
(GYMNOSPERMS)

The pattern of relationships in cladograms 1 and 2 is very similar. In both, seed plants are interpreted as a monophyletic group defined by the presence of an integument (character 9.4) with a well-differentiated micropyle (character 9.5) surrounding a megasporangium with a single functional megaspore mother-cell (character 9.3) and having a free nuclear phase in embryogenesis (character 9.2, secondarily cellular in *Welwitschia* and angiosperms). The possibility of seed plant polyphyly suggested by Arnold (1948), Beck (1981), and Chaloner et al. (1977) is not supported by the cladogram, but a full analysis of this problem would have to take into account additional progymnosperms and primitive seed plants that currently are only poorly known.

*Lyginopteris* is resolved by both cladograms as the sister taxon to all other seed plants considered. However, the characters on which this division is based are not strong. Distal pollen aperture (character 9.15) is particularly problematic (see below), and although *Lyginopteris* probably had a tetrahedral tetrad of megaspores, the distribution of tetrahedral and linear tetrads in other fossil plants is not well known.

A close relationship between the Carboniferous pteridosperms and cycads has been recognized by many authors. Arnold (1953) and Scott (1923) suggested that cycads were closely related



TABLE 9. Continued.

| <i>Ginkgo</i> | <i>Cal-<br/>listo-<br/>phyton</i> | Pelta-<br>sperms | Glos-<br>sopter-<br>ids | <i>Cay-<br/>tonia</i> | Co-<br>rysto-<br>sperms | Bennet-<br>tiales | <i>Pent-<br/>oxylon</i> | <i>Gnetum</i> | <i>Wel-<br/>witschia</i> | <i>Ephed-<br/>ra</i> | Angio-<br>sperms |
|---------------|-----------------------------------|------------------|-------------------------|-----------------------|-------------------------|-------------------|-------------------------|---------------|--------------------------|----------------------|------------------|
| —             | —                                 | —?               | —                       | —?                    | —?                      | —?                | —?                      | —             | —                        | —                    | +                |
| —             | —?                                | —?               | —?                      | —?                    | —?                      | —?                | —?                      | —             | —                        | —                    | +                |
| —             | —?                                | —?               | —?                      | —?                    | —?                      | —?                | —?                      | —             | —                        | —                    | +                |
| —             | —?                                | —?               | —?                      | —?                    | —?                      | —?                | —?                      | —             | —                        | —                    | +                |

to lyginopterid pteridosperms, while Delevoryas (1955), Stewart (1983), and Wordsell (1906) have favored a closer, even ancestor-descendant, relationship from medullosans. Cladogram 1 supports the view that medullosans and cycads are sister taxa based on the double vascular system in the ovule (character 9.7). This assumes that the *Lagenostoma* cupule has no homology in the cycad ovule, and that the chalazal pad of vascular tissue in the ovules of conifers, cordaites (*Cordaixylon*, *Mesoxylon*), and *Callistophyton* is not the remains of a previous inner integument (see character 9.7). In cladogram 2 the position of cycads and medullosans relative to each other, and relative to all other seed plants considered (except *Lyginopteris*), is not resolved. Both cladograms suggest that the apparent absence of axillary branching in cycads (character 9.8) is the result of secondary loss, and that axillary branching is a potential seed plant synapomorphy. Loss of axillary branching may be one result of the specialized pachycaul habit of extant cycads. The relationships of *Spermopteris*, *Phasmatocycas*, and *Archaeocycas* to cycads (Mamay, 1976) are discussed later in this paper. Similarly, both cladograms suggest that the protostele of *Quaestora* is reduced from the eustele that characterizes all other seed plants considered. This conclusion may have to be modified if it could be demonstrated that cycads and medullosans were closely related to aneurophytalean progymnosperms (protostelic) as suggested by some authors (e.g., Stewart, 1983).

The evidence for a close relationship between conifers and cordaites was presented convincingly by Florin (1951) and has been accepted widely by subsequent authors (Mapes & Rothwell, 1984; Rothwell, 1982b). Recently, however, Beck (1981: 193) has suggested “that the

Cordaitales and Lebachiaceae represent independent lines of evolution originating from *Archaeopteris* or some closely related, similar progymnosperm.” This hypothesis would require at least a biphyletic origin of seed plants that is not supported by the analyses in this paper. The cladograms reflect the views of Florin and other authors. They suggest that conifers and cordaites are more closely related to each other than either is to *Archaeopteris* on the basis of several derived characters: single functional megaspore mother-cell per megasporangium (character 9.3), integument (character 9.4), micropyle (character 9.5), axillary branching (character 9.8), saccate pollen (character 9.9), flattened ovules (character 9.10), megasporophylls borne on short fertile shoots in the axils of bracts (character 9.13), and ovulate short shoots aggregated into an “inflorescence” (character 9.14). Rothwell (1982b) has similarly emphasized the importance of these characters in his analysis of Beck’s hypothesis. The microsporangiate “inflorescence” of *Cordaites* is a feature that has been suggested as a specialization precluding an ancestral relationship to the conifers (Beck, 1981; Pant, 1977b). In cladistic terms this character would be a synapomorphy of cordaites but would not obviate a close relationship with conifers. The difficulty only arises when the relationship between the two groups is viewed as that of an ancestor and descendant. Similar arguments could be applied to other, possibly unique, specializations of cordaites listed by Beck (1981: 215) (leaf morphology, bilaterally symmetrical distichous inflorescences).

The closest relatives of *Ginkgo* have long been thought to be conifers and cordaites (Chamberlain, 1935; Emberger, 1954; Pant, 1977b), and this is supported by both cladograms in which *Ginkgo* is placed as the sister taxon to the conifer



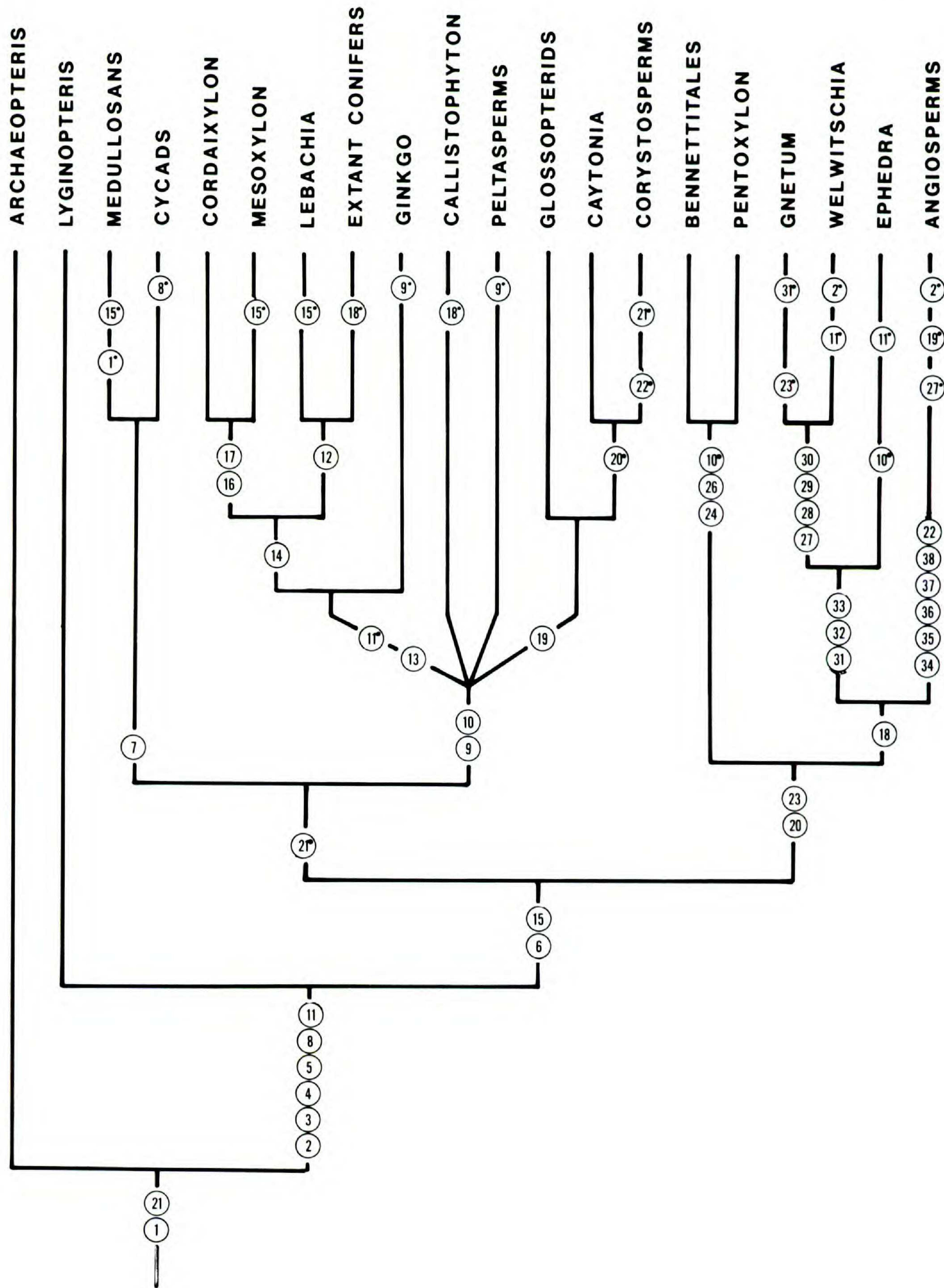


FIGURE 20. Relationships between major groups of seed plants. Strict consensus tree derived from five equally parsimonious cladograms constructed from version one of the data matrix. In this analysis the “cupules” of Bennettitales and *Pentoxylon* were not coded as homologous to the “cupules” of glossopterids, *Caytonia*, corytosperms, and angiosperms. Bennettitales and *Pentoxylon* were coded as plesiomorphic for characters 9.19 and 9.22, and character 9.25 was excluded as redundant. Total characters 37, character state transitions 61. A dot next to the number indicates homoplasy.



plus the cordaite clade. The synapomorphy of the *Ginkgo* plus conifer plus cordaite clade is the presence of megasporophylls on an axillary fertile shoot (character 9.13). The morphological interpretation presented earlier (p. 749) of the *Ginkgo* ovulate reproductive structure is therefore critical. There is no support in the analysis of characters presented here for Meyen's (1984) view that *Ginkgo* and related plants constitute a very distinct major lineage in seed plant evolution. *Ginkgo* is resolved as more closely related to conifers and cordaites than to any of the taxa included by Meyen in his Ginkgoopsida. Similarly, although *Ginkgo* shares some features such as zooidogamy and the long free nuclear phase of embryogenesis with the living cycads (Stewart, 1983: 319), in cladistic terms these are primitive characters that do not indicate close phylogenetic relationship (Chamberlain, 1935: 216).

Rothwell (1981) discussed two possibilities for the phylogenetic relationships of *Callistophyton*: either it is more closely related to conifers and cordaites than it is to other pteridosperms, or the similarities with conifers and cordaites are because of parallel evolution. He rejected both and suggested a position intermediate between pteridosperms and cordaites or conifers. Both cladograms reflect the difficulties in resolving the precise phylogenetic relationship of *Callistophyton* and have a polychotomy involving cordaites plus conifers, *Callistophyton*, peltasperms, and the glossopterid plus *Caytonia* plus corystosperm clade. These four groups are themselves united by flattened seeds (character 9.10) and saccate pollen (lost secondarily in peltasperms, character 9.9).

One advanced character that may ultimately be important in assessing the relationships of *Callistophyton* is the presence of pollen with a distal aperture. In both cladograms it is methodologically more parsimonious to interpret the proximal germinal apertures in medullosans, *Mesoxylon*, and *Lebachia* as reversals from distal germination primitive for all seed plants except *Lyginopteris* (a total of three reversals). However, from a botanical perspective such reversals seem unlikely and most paleobotanists would probably view the prepollen of medullosans, *Mesoxylon*, and *Lebachia* as retention of a primitive feature. If this view is adopted it necessitates five (cladogram 2) or six (cladogram 1) independent origins of distal germination. Chaloner (1970a) recognized that the switch from proximal to distal germination had occurred sev-

eral times in seed plant evolution, but the extent of this parallelism is of considerable interest. It suggests that detailed studies of pollen ontogeny might detect different mechanisms of aperture formation, and it clearly indicates that pollen with a distal aperture is not a good synapomorphy of seed plants as might be concluded from a cladistic analysis restricted solely to extant gymnosperms.

At the same level as *Callistophyton* in the cladogram the systematic relationships of peltasperms are unresolved; but the other group incorporated at this polychotomy is the glossopterid plus *Caytonia* plus corystosperm clade defined by the presence of a "cupule" (character 9.19). Within this group *Caytonia* and corystosperms are more closely related to each other than either is to glossopterids based on the poorly developed acid-resistant megaspore membrane (character 9.20). These relationships among "Mesozoic seed ferns" are maintained in both cladograms.

The relationships of *Pentoxylon* previously have been considered enigmatic. Frequently the genus has been viewed as a peculiar and isolated gymnosperm of uncertain phylogenetic relationship (Andrews, 1961; Stewart, 1983) though various similarities with other groups of seed plants have been pointed out. For example, monosulcate pollen occurs in cycads, *Ginkgo*, and the Bennettitales, while pycnoxylic conifer-like wood is a generalized feature within seed plants as a whole. Other authors (e.g., Ehrendorfer, 1971) have suggested a close relationship between *Pentoxylon* and the Bennettitales. In the analysis given here two relatively advanced characters are useful in establishing the phylogenetic relationships of *Pentoxylon*: the "flower-like" arrangement of the microsporophylls (character 9.23), which also occurs in Bennettitales, Gnetales, and angiosperms; the aggregation of the ovules into a head (character 9.26), which otherwise occurs only in the Bennettitales, and the structural similarity of bitegmic bennettitalean and *Pentoxylon* ovules (characters 9.19, 9.25, 9.26). If the interseminal scales of Bennettitales are accepted as being derived ontogenetically and phylogenetically from "cupule" primordia (characters 6.1, 9.19) then the existence of fully fertile ovulate heads like those of *Pentoxylon*, which lack interseminal scales, is a straightforward and reasonable prediction. This general view (though before *Pentoxylon* had been studied) was expressed by Wieland (1906: 120). The stomata of



*Nipaniophyllum* (*Pentoxylon*) were originally described by Sahni (1948: 56) as syndetocheilic, and they deserve careful reexamination to clarify the range of variation which they exhibit and to establish their precise similarities and differences with those of the Bennettitales. It is also interesting that the anticlinal flanges of *Nipaniophyllum* leaf cuticles are finely sinuous, like those of most Bennettitales.

A close relationship between Bennettitales and cycads is not supported by the cladogram, although the two groups frequently have been treated together on the basis of their leaf morphology and the similar habit of cycads and *Cycadeoidea* (Wieland, 1906, 1916). Both cladograms suggest that these similarities are the result of convergence. Many authors (Arber & Parkin, 1907: 51; Arnold, 1953: 58; Stewart, 1983) have recognized that the cycad plus Bennettitales group is artificial and probably does not reflect close phylogenetic relationship. The two groups are treated together primarily for reasons of convenience and tradition, but according to the analysis in this paper even the general designation of the Bennettitales as "cycadophytes" obscures their probable phylogenetic relationships with other taxa. On the basis of the characters given here, the two groups are very far apart.

In both cladograms the Bennettitales plus *Pentoxylon* clade is resolved as a sister group to a clade comprising the angiosperms plus Gnetales exactly as proposed by Arber and Parkin (1908). The probability of a close relationship between the Bennettitales and Gnetales frequently has been suggested (Arber & Parkin, 1907, 1908; Martens, 1971: 269; Takhtajan, 1969: 17; Thoday, 1911), but at this level of analysis the cladogram does not support the view that the gnetalean "flower" is a highly reduced bisexual bennettitalean "flower" consisting of a single ovule or that the Gnetales and Bennettitales are sister taxa. It is nevertheless possible that a more detailed character analysis might place the Gnetales as a relatively advanced monophyletic group within the bennettitalean clade. If this could be supported then a bennettitalean origin for the gnetalean "flower" would be more plausible. In this case the bennettitalean "perianth" (character 9.33) may be interpreted as homologous to the opposite bracteoles of the Gnetales, and the "slight protruberance slightly below the epicotyl" in *Cycadeoidea* embryos (Crepet, 1974: 158) could be compared to a poorly developed "feeder" in *Welwitschia* or *Gnetum* (character 9.30).

Other similarities between the Bennettitales and Gnetales include the details of the micropyle and seeds (Berridge, 1911; Thoday, 1911), paracytic stomata, bisporangiate flowers, the possible presence of vessels (Krassilov, 1984), and the presence of a long micropylar tube. Cladogram 2 also supports the view that the apparent absence of a true outer integument in Gnetales is most easily explained as a secondary loss.

The main alternative to a bennettitalean or angiosperm relationship of the Gnetales is the possibility of a close relationship between *Ephedra* and cordaites (Eames, 1952). Eames emphasized the difference between *Ephedra* versus *Gnetum* and *Welwitschia*. The cladogram supports the view that *Gnetum* and *Welwitschia* are more closely related to each other than either is to *Ephedra* based on the reduced male gametophyte (character 9.27), the tetrasporic female gametophyte (character 9.28), the lack of archegonia (character 9.29), and the presence of a "feeder" in the embryo (character 9.30; see also p. 766). However, contrary to Eames (1952) the cladogram suggests that the Gnetales are monophyletic and united by fundamentally similar reproductive structures (character 9.33), vessels (character 9.32), and possibly by their distinctive, ribbed pollen (character 9.31). Eames based his discussion mainly on the fertile axillary shoot that occurs in both Gnetales and cordaites, and his views hinge in particular on an interpretation of the ovules in *Ephedra* as appendicular rather than cauline. The other *Ephedra*-cordaite similarities cited by Eames (1952) are interpreted here as primitive features within seed plants (pycnoxylic wood, anomocytic stomata) or independently derived in the spermatophyte clade (non-megaphyllous leaves).

In most features already discussed cladograms 1 and 2 scarcely differ, but the most prominent and almost the sole effect of interpreting the other integument of Bennettitales and *Pentoxylon* as homologous with the "cupule" in glossopterids, *Caytonia*, corystosperms, and angiosperms is to reposition the Bennettitales plus *Pentoxylon* plus Gnetales plus angiosperm clade as the sister group to the corystosperms. Under this interpretation the orthotropous bitegmic ovules of Bennettitales and *Pentoxylon* may be considered the ultimate product of a reduction series involving the *Caytonia* megasporophyll with several "cupules" and several seeds in each; and the corystosperm megasporophyll with fewer "cupules" each containing a single seed. The bennettitalean



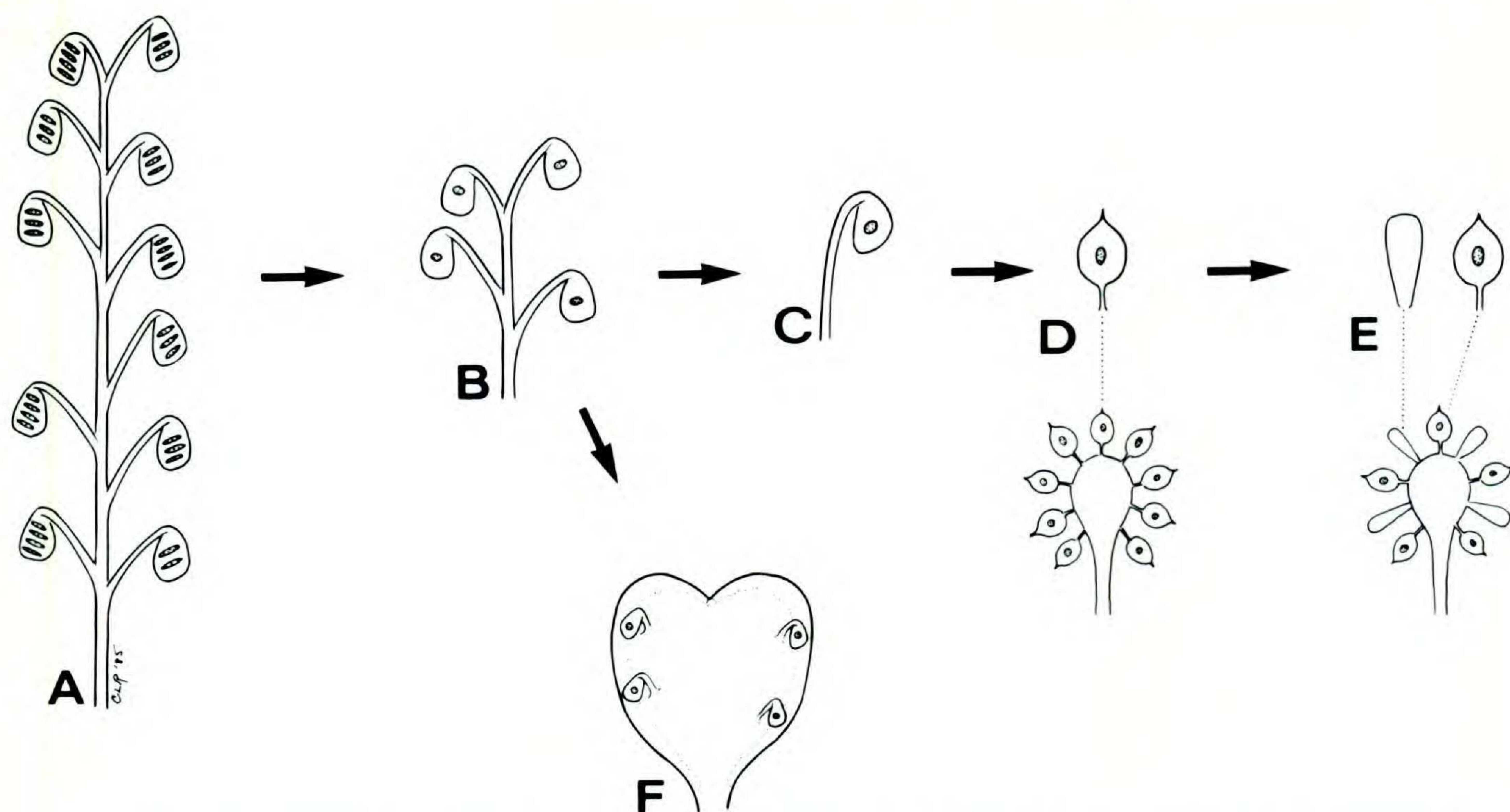


FIGURE 21. Suggested homologies between megasporophylls of *Caytonia*, corystosperms, *Pentoxylon*, Bennettitales, and angiosperms.—A. *Caytonia*-like megasporophyll with several “cupules,” each containing numerous ovules.—B. Corystosperm-like megasporophyll with few uniovulate “cupules.”—C. Hypothetical recurved “unicupulate” megasporophyll containing one ovule.—D. Erect (“orthotropous”) “unicupulate” megasporophylls containing a single ovule, aggregated into a head as in *Pentoxylon*.—E. Head of fertile and sterile “unicupulate,” uniovulate megasporophylls as in Bennettitales. Sterile megasporophylls forming interseminal scales.—F. Angiosperm carpel opened and viewed adaxially. See text for further explanation.

or *Pentoxylon* ovule would be interpreted as a highly reduced megasporophyll of one “cupule” containing a single seed (Fig. 21, see also Thomas, 1955: 655). In my view the only major argument against this interpretation is the orthotropous orientation of bennettitalean and *Pentoxylon* “cupules” versus the recurved “cupules” of *Caytonia* and corystosperms. Clearly it would be of considerable interest if the predicted (but unknown) recurved bitegmic ovules were detected in primitive Bennettitales.

In favor of the relationship suggested in cladogram 2 is the similarity of ovule structure and cuticles in *Caytonia*, corystosperms, Bennettitales, and *Pentoxylon*. Additional evidence is provided by the similarity between *Rhexoxylon* (probable corystosperm stem) and *Pentoxylon*. Both have a “polystelic” arrangement of vascular tissue and also show an identical pattern of leaf-trace origin (Stewart, 1983: 312). On the basis of this slim evidence I currently favor cladogram 2 over cladogram 1 as most likely approaching the true phylogenetic relationships of seed plants, and this view is also more broadly consistent with the stratigraphic evidence. Cladogram 1 places the origin of four fundamentally Mesozoic groups (Bennettitales, *Pentoxylon*, Gnetales, and

angiosperms) at a level equivalent to the origin of major Paleozoic groups such as medullosans and cordaites. Further work is clearly necessary to supplement our knowledge of characters and plants relevant to the competing hypotheses of cladograms 1 and 2. In particular, a detailed comparative study of the “cupules” of *Vardekloeftia* (Harris, 1932b), *Bennetticarpus crossospermus* (Harris, 1932b), other Bennettitales (Stopes, 1918; Wieland, 1906: 120; Kräusel, 1949), *Pentoxylon*, and corystosperms is a primary requirement.

In addition to the particular questions of relationship already considered, the cladograms raise two general issues: are the pteridosperms a phylogenetically useful group, and how well do existing classifications of seed plants reflect phylogenetic relationships? The extreme heterogeneity of the “pteridosperms” is clearly demonstrated in both cladograms. The relationships of medullosans, *Lyginopteris*, *Callistophyton*, peltasperms, glossopterids, *Caytonia*, and corystosperms are extremely diverse, and there is no pair of pteridosperm taxa that together constitute a monophyletic group in both cladograms. Generally the concept of the pteridosperms has been used intuitively with little attempt at rigorous



TABLE 10. Previous classification of gymnosperms. Extinct taxa indicated with an asterisk.

| Chamberlain, 1935 | Bierhorst, 1971   |
|-------------------|-------------------|
| Cycadophytes      | Cycadopsida       |
| *Cycadofilicales  | *Pteridospermales |
| *Bennettitales    | Cycadales         |
| Cycadales         | *Cycadeoidales    |
| Coniferophytes    | *Caytoniales      |
| *Cordaitales      | Coniferopsida     |
| Ginkgoales        | *Cordaitales      |
| Coniferales       | Coniferales       |
| Gnetales          | Taxales           |
|                   | Ginkgoales        |
|                   | Gnetopsida        |
|                   | Ephedrales        |
|                   | Gnetales          |
|                   | Welwitschiales    |
|                   | Angiospermopsida  |

definition. However, Townrow (1962a: 316) offered a more precise circumscription defining the pteridosperms as “gymnospermous plants with leaves, pollen- and seed-bearing organs pinnate. Reproductive structures not aggregated into cones or flowers.” This defines the pteridosperms entirely in terms of pinnately organized leaves, microsporophylls, and megasporophylls (character 9.11), which are all generalized features within most groups of seed plants. On this definition the pteridosperms are merely the residue of seed plants after taxa with “cones” (cycads, conifers, cordaites, *Pentoxylon*) and taxa with “flowers” (presumably Bennettitales, Gnetales, and angiosperms) have been removed. The group is defined by exclusion and primitive characters. For phylogenetic purposes the current concept of the pteridosperms is valueless and has been a major source of confusion in attempts to analyze the phylogenetic relationships of seed plants.

The pattern of relationships expressed in the cladogram can be usefully compared with views expressed in the classifications of previous authors. It should, however, be recognized that classifications may be viewed as having many purposes, and not all were intended to reflect phylogenetic relationships. Considering only extant gymnosperms the cladogram compares favorably with the classification of Chamberlain (1935) (Table 10). Chamberlain divided the extant gymnosperms into two groups, cycadophytes, in which he placed the cycads, and coniferophytes, in which he included the conifers, *Ginkgo*, and Gnetales. He clearly recognized the distinctiveness of the cycads, and that the co-

nifers, *Ginkgo* and Gnetales were more closely related. Bierhorst (1971) (Table 10) separated the Gnetopsida from the Coniferopsida, although he acknowledged that they are probably more closely related than either is to cycads. However, when the comparisons are extended to include fossil plants, the cladogram conflicts with the classifications of Chamberlain (1935) and Bierhorst (1971). Both these authors recognized the Pteridospermales (Cycadofilicales) and the Cycadeoidales (Bennettitales) as two groups within the Cycadopsida (Cycadophytes). The heterogeneity of the pteridosperms already has been discussed, and according to cladogram 1, conifers, cordaites, and *Ginkgo* are more closely related to cycads than to Bennettitales. In cladogram 2 the Bennettitales are more closely related to conifers, cordaites, *Ginkgo*, and Gnetales. Bierhorst (1971) also included *Caytonia* in the Cycadopsida. In both cladograms *Caytonia* is more closely related to conifers, cordaites, and *Ginkgo*. The results presented here suggest that in order for the cycadophytes to be considered a monophyletic group, it should probably include only the medullosans and cycads.

If the cycadophytes of Chamberlain’s system are redefined in restricted form, the “coniferophytes” according to both cladograms expand to include *Callistophyton*, glossopterids, *Caytonia*, and corystosperms. In cladogram 2 the Bennettitales, *Pentoxylon*, Gnetales, and angiosperms are also included in the coniferophyte clade. In this context many of the traditional distinctions between the cycadophytes and coniferophytes break down, and the “coniferophytes” no longer include only forms with profuse branching, small simple leaves, small pith and cortex, and pycnoxylic secondary xylem (Foster & Gifford, 1974: 385). If the relationships in cladogram 2 are accepted, it may be more useful to recognize a broad group (“platysperms”) defined by the presence of flattened ovules. Radiospermic ovules has been one of the characters traditionally used to link the cycads with the Bennettitales and even has been used to suggest a relationship between the Gnetales and medullosans (Rodin & Kapil, 1969: 429). Under the interpretation in cladogram 2, the Bennettitales and Gnetales are only secondarily radiospermic, and some, such as *Vardekloeftia* and *Ephedra*, are platyspermic. There is, in any case, very little resemblance between the small, poorly vascularized ovules of the Bennettitales and the large, doubly vascularized ovules of cycads. According to the analysis of characters



in this paper, the radiospermy of cycads, medullosans, and *Lyginopteris* is not homologous with the secondary "pseudoradiospermy" of Bennettitales and Gnetales.

#### DISCUSSION AND INTERPRETATION (ANGIOSPERMS)

The angiosperms along with the Gnetales and the Bennettitales plus *Pentoxylon* clade form a monophyletic group. In cladogram 1 this clade is placed as the sister group to all other seed plants considered (except *Lyginopteris*). In cladogram 2 the corystosperms are the sister group to the Bennettitales plus *Pentoxylon* plus Gnetales plus angiosperm clade. This second pattern of relationships is broadly consistent with the view that the "Mesozoic seed ferns" were important in angiosperm origins (Andrews, 1961; Doyle, 1978; Gaussen, 1946; Retallack & Dilcher, 1981; Stebbins, 1974; Stewart, 1983) and reconciles this idea with the suggestions of Arber and Parkin (1907, 1908) concerning the relationships of angiosperms to the Gnetales and Bennettitales.

The analysis of characters presented here does not address the possibility that the angiosperms are polyphyletic (Hughes, 1976, 1977; Krassilov, 1973, 1975; Meeuse, 1966) and accepts the traditional view that the angiosperms are monophyletic (Cronquist, 1968; Takhtajan, 1969). In cladistic terms polyphyly could only be supported if a group of flowering plants could be shown to be more closely related to some group of gymnosperms than to other flowering plants. This has never been explicitly demonstrated, but is implicit in Krassilov's (1977b) suggestion that there are three major mid-Cretaceous angiosperm "lineages," the Hamamelidales, Laurales, and monocotyledons, that are "rooted" in the Dirhopalostachyaceae, Caytoniales, and Czekanowskiales, respectively. In both cladograms the angiosperms could be justified as monophyletic by five characters (9.34–9.38; see also Hill & Crane, 1982). It should, however, be recognized that most of these features are difficult to assess even in living plants, that most species in the Magnoliidae are relatively poorly understood, and that there are real problems of sampling in such a large group.

An interesting aspect of the cladogram is that the flowering plants are more closely related to Gnetales than any other group of gymnosperms. This view was advocated in the earlier part of

this century (Arber & Parkin, 1908) but has been out of favor for over 50 years, apparently for two principal reasons. The first is the apparent difficulty of "transforming" the ovulate structures of the Gnetales into an angiosperm carpel. Although this has been attempted by several authors (Meeuse, 1966; Thompson, 1916), the results have been unconvincing and usually have involved comparison with the ovary in some "Amentiferae" that are more likely to represent secondary modifications within the flowering plant clade. These hypotheses also have been unable to account for the origin of the conduplicate carpel.

The second reason stems from the widely accepted view that vessels arose independently in the Gnetales and angiosperms (see earlier discussion of characters 1.6, 9.32). This view has been so influential that, even when the many similarities between Gnetales and angiosperms have been acknowledged, the conclusion has been that "the evidence of vascular anatomy strongly controverts any suggestion of relationships" (Cronquist, 1968: 43).

Both of these problems seem to arise out of the preoccupation with identifying angiosperm ancestors and the apparent impossibility that the Gnetales could have fulfilled this role. From a cladistic standpoint, such an ancestor-descendant relationship is untenable; some of the similarities between the two groups indicate a close phylogenetic relationship, but each has its own specializations with neither being ancestral to the other (see also Arber & Parkin, 1908; Just, 1948). Interestingly too, several of the gnetalean features that appear to be present in flowering plants (e.g., the dicotyledonous leaves of *Gnetum*) may well be secondary advances *within* the gnetalean clade.

In both cladograms, the Gnetales and angiosperms are resolved as sister groups (cf. Arber & Parkin, 1908; Just, 1948) but exhibit some parallelisms. Angiosperms share several derived features with *Gnetum* and *Welwitschia*, including the poorly developed male gametophyte (character 9.27), embryogenesis with no free nuclear phase (character 9.2), precocious differentiation of integuments at the time of megasporogenesis (Crepet, 1974: 163), presence of astrosclereids (Bierhorst, 1971: 475), and the occurrence of paracytic stomata that, according to Baranova (1972), are primitive within angiosperms. In addition, angiosperms and *Gnetum* are similar in leaf morphology and in having a



partially (*Gnetum*) or completely coenocytic (angiosperms) female gametophyte at fertilization. Further similarities between the Gnetales and angiosperms, that require more detailed examination, are similarities in chemistry (Gottlieb & Kubitzki, 1984) particularly of the wood (Gibbs, 1958; McLean & Evans, 1934; Melvin & Stewart, 1969; Nishio, 1959), the occurrence of laticifers (Muhammad & Sattler, 1982), the small chromosomes, and the occurrence of polyploidy in *Ephedra* (Ehrendorfer, 1976). Ehrendorfer estimates the base chromosome number of Gnetales as  $n = 7$ , the same value as that estimated for the base number of angiosperms (Raven, 1975).

Arber and Parkin (1908: 513) explicitly recognized a sister-group relationship between the angiosperms and Gnetales, with the Bennettiales as a sister group to both. The Bennettiales were an important factor in the development of the Anthostrobilus theory of the angiosperm flower (Arber & Parkin, 1907) and were part of the justification for considering the "Ranalian plexus" as the most primitive living flowering plants. The cladogram provides an explicit base from which to examine further the idea that the Bennettiales, like *Pentoxylon* and Gnetales, are closely related to flowering plants and from which to pursue the functional parallelisms in terms of pollination and dispersal biology that can be traced in these clades.

Other hypotheses for the origin of the angiosperms are not supported by the distribution of characters in the cladogram. The cupules of lyginopterid seed ferns are not treated as homologous with those of "Mesozoic seed ferns" (character 9.19) and the cladogram lends no a posteriori support to this idea. Lyginopterid cupules therefore seem unlikely to be helpful in any parsimonious explanation of the origin of the second integument or carpel in angiosperms (Long, 1966, 1977). Indeed, results from a PAUP analysis of Table 9 in which the cupule of *Lyginopteris* is scored as homologous with the "cupules" of glossopterids, *Caytonia*, and corystosperms and the second integument of Bennettiales, *Pentoxylon* and angiosperms, place *Lyginopteris* in various highly derived positions inconsistent with other aspects of its morphology (and stratigraphic position). The suggestion that the carpel evolved by inrolling of a cycad-like megasporophyll (Mamay, 1976) is also unsupported by the relative positions of cycads and angiosperms in the cladogram. Inrolling of a simple megasporophyll

would, in any case, only produce a carpel containing unitegmic ovules. Additionally, some of the plants (*Spermopteris*, *Phasmatocycas*) on which this hypothesis is based are interpreted here as platyspermic, and possibly more closely related to *Callistophyton*, the Mesozoic seed ferns, Bennettiales, Gnetales, and angiosperms, rather than to cycads (see below).

Similarly, the notion that the angiosperms are cycadopsid seed plants (Doyle, 1978; Stewart, 1983) is not supported by the cladogram. This idea can be traced to the view that the seed ferns are uniformly a cycadopsid group. In fact, the accretionary historical development of the seed-fern concept, and their original designation as "Cycadofilicales," has obscured their phylogenetic heterogeneity. In my view the seed ferns include both cycadopsid and coniferopsid forms (p. 776), and it is the latter taxa that are more closely related to angiosperms.

#### PHYLOGENETIC RELATIONSHIPS OF OTHER FOSSIL GYMNOSPERMS

##### *EREMOPTERIS*, *NYSTROEMIA*, AND SIMILAR PLANTS

Leaves, seeds, and probable microsporangia of *Eremopteris* were described by Delevoryas and Taylor (1969) from the Upper Pennsylvanian of Pennsylvania. The bipinnate leaves were closely associated with stalked flattened ovules. Each ovule possessed a pair of prominent apical "horns" and some showed probable well-developed megaspore membranes. Ovules and microsporangia of *Nystroemia pectiniformis* from the Permian of China (Halle, 1929) are similar to those of *Eremopteris*. Although important details of both *Eremopteris* and *Nystroemia* are unknown, the flattened ovules, combined with the lack of a "cupule" or conifer-cordaite-like inflorescence, suggests a combination of relatively advanced and primitive features similar to that seen in *Callistophyton* and peltasperms.

Permian pinnately organized leaves bearing ovules on the lamina or at the margin have been described as "callipteroid" (Mamay & Watt, 1971). *Tinsleya* (Mamay, 1966), *Sphenopteris tenuis* (Halle, 1929), *Emplectopteris triangularis* (Halle, 1929), and *Archaeocycas* (Mamay, 1976) are too poorly understood for detailed evaluation of their systematic relationships. It is, however, of interest that microsporophylls thought to be associated with these callipterid plants produced bisaccate pollen (see Mamay, 1966: 1).



## SPERMOPTERIS, PHASMATOCYCAS, SOBERHEIMIA

*Spermopteris coriacea* (Goeppert) Cridland & Morris (1960) from the Upper Pennsylvanian of Kansas consists of entire-margined taeniopterid leaves bearing ovules on the abaxial surface. The ovules are confined to the distal portions of the leaf and form a row on either side of the midvein. They were oriented at right angles to the midvein with their micropyles arranged approximately along the margin. They were probably flattened with a distinct micropylar notch.

*Phasmatocycas kansana* Mamay (1976) is a megasporophyll with sessile ovules borne in two lateral rows. Distally the megasporophyll may have expanded into a lamina with taeniopterid venation (Mamay, 1976, but see Kerp, 1983). The ovules were flattened (Stewart, 1983: 283), had a shallowly bifid, notched apex similar to those of *Spermopteris*, a blunt, funnel-shaped micropyle, and a thick megaspore membrane. Recently collected material from Kansas (Pfefferkorn, pers. comm.) also has flattened ovules.

*Soberheimia jonkeri* Kerp (1983) from the Permian of Germany is similar to *Spermopteris* and *Phasmatocycas*. It is a leaf-like, bilaterally symmetrical structure with two rows of lateral organs interpreted as seeds. The lamina is thought to have been lobed with expansions between the seeds.

Mamay (1976) interpreted *Spermopteris* and *Phasmatocycas* as important plants in the evolution of cycads. According to the analysis of characters given here, a close relationship to cycads is unlikely. Cycads and medullosans do not have platyspermic seeds and, as in *Eremopteris* and *Nystroemia*, the possession of this feature, combined with the lack of a conifer-cordaite-like inflorescence or "cupules," is a combination of advanced and primitive features similar to that in *Callistophyton* and peltasperms.

## VOJNOVSKYALES

The Vojnovskyales are a group of Permian plants described from Asia, North and South America, and Africa (Krassilov & Burago, 1981). Leaves of *Vojnovskya* (*Nephrolepis*) are fan-shaped and resemble those of the enigmatic Triassic plant *Sanmiguelia* (Ash, 1982; Becker, 1972; Tidwell et al., 1977) in the plications of the lamina and the lack of a clearly differentiated petiole. The reproductive structures are poorly understood but apparently consisted of "heads"

with several platyspermic ovules and numerous elongated scales. These scales have been interpreted as microsporophylls but were probably sterile (Maheshwari & Meyen, 1975). Comparison of these few characters of the Vojnovskyales with the cladogram suggests that the combination of platyspermic ovules (character 9.10) clustered together into heads (character 9.26) could indicate a possible relationship with Bennettitales and *Pentoxylon*. In view of this possibility, a detailed study of the stomata of *Vojnovskya* would be useful, and it would be of considerable interest to compare the scales on *Vojnovskya* "heads" with the interseminal scales of Bennettitales (Harris in Mamay, 1978).

## PUTATIVE GNETALES

The Gnetales currently have no well-established macrofossil record (Taylor, 1981a), although this may reflect difficulties of recognition rather than real absence (Arber & Parkin, 1908; Hill & Crane, 1982; Crane & Upchurch, work in progress). Upchurch and Crane (1985) describe a probable gnetalean with attached leaves and seeds from the Lower Cretaceous Potomac Group of Virginia, and pollen resembling that of extant *Ephedra* and *Welwitschia* is widely distributed during the Triassic and early Cretaceous. Recent transmission electron microscope studies of this "gnetalean" pollen have shown that the similarities also extend to the granular exine structure (Trevisan, 1980). Little is known of the plants that produced these grains. The Triassic dispersed pollen *Equisetosporites chinleana* was referred to *Ephedra* by Scott (1960) and has subsequently been demonstrated within microsporangiate cones (*Masculostrobis clathratus* Ash, 1972b; see Zavada, 1984, for details of pollen). The cones consisted of a main axis bearing spirally arranged microsporophylls with microsporangia on the undersurface of an expanded distal lamina. *Bosea indica* is a further microsporangiate structure from the Middle Triassic of Nidpur, India (Srivastava, 1973). It consisted of a stout axis bearing opposite or sub-opposite microsporophylls with unilocular sporangia on the lower surface. The sporangia produced non-saccate, monosulcate pollen with pronounced longitudinal ribs. Neither *M. clathratus* nor *B. indica* is similar to the microsporangiate structures of *Ephedra*, but both could be interpreted as similar to *Pteruchus* in which both dorsiventral and



helical arrangement of microsporophylls occurs (Pant & Basu, 1973). On the basis of cuticular structure Srivastava (1973) suggested that *B. indica* might be part of the plant that produced *Lepidopteris indica* leaves. These similarities with Gnetales and corystosperms require more detailed examination but are of considerable interest in view of the relative positions of these two groups in the cladograms.

A further possible macrofossil record of gnetalean-like plants is *Hexagonocaulon minutum* from the Upper to Middle Triassic of the South Shetland Islands. *Hexagonocaulon minutum* Lacey and Lucas (1981) was established for a large number of small in situ axes, each 0.5–4 mm in diameter. The axes bore alternating whorls of three scale-like bilobed appendages at the nodes. Nothing is known of the reproductive structures, but anatomically they share some similarities with *Equisetites* and *Ephedra* (Lacey & Lucas, 1981).

Another fossil for which a gnetalean relationship has been suggested is the dispersed pollen *Eucommiidites*. *Eucommiidites troedsonii* was described first from the early Jurassic of southern Sweden (Erdtman, 1948) and interpreted as a tricolpate angiosperm grain with unequally developed colpi. Based on analyses of the symmetry, Couper (1956, 1958) suggested that a gymnospermous relationship was more likely, and Hughes (1961) interpreted the grain as distally monosulcate with a proximal zonosulcus. Pollen wall structure of *Eucommiidites* is granular (Doyle et al., 1975), but in some forms there are "pillar-like elements" in the pollen wall (Trevisan, 1980). The gymnospermous affinity of *Eucommiidites* was confirmed by its pollen wall structure (Doyle et al., 1975) and by its occurrence in the micropyles of dispersed seeds from the Lower Cretaceous (Wealden) of southern England (Hughes, 1961), the Lower Cretaceous Patuxent Formation of Virginia (Brenner, 1967), and the Upper Liassic of Poland (Reymanówna, 1968). van Konijnenburg-van Cittert (1971) has described a microsporangiate cone-like structure from the Jurassic of Yorkshire that produced *Eucommiidites* pollen in numerous microsporangia on the adaxial surface of a microsporophyll.

Knowledge of *Eucommiidites* is therefore too fragmentary to permit a detailed evaluation of relationships. However, the granular pollen wall (character 9.21) and the occurrence in ovules with an elongated micropyle suggests the possibility of a relationship with corystosperms, Gnetales, Bennettitales, or *Pentoxylon*. Similar views have

been expressed by Hughes (1961), Trevisan (1980), and Doyle et al. (1975). Against this suggestion is the occurrence of a well-developed megaspore membrane in the ovules (Reymanówna, 1968). Further information on the plants producing *Eucommiidites* is clearly required.

#### LEPTOSTROBUS

*Leptostrobus* is an ovulate reproductive structure of Jurassic and Lower Cretaceous age. It consists of an axis bearing small scale leaves at the base and widely separated "capsules" containing ovules in the upper region (Harris, 1951a; Harris et al., 1974; Krassilov, 1977b). The "capsules" are sessile and two-valved, with each valve containing a single row of three to eight small ovules. The ovules are poorly known, but were arranged with their micropyles facing the cone axis, and had a resistant megaspore membrane. Based on field association and cuticular similarity, *Leptostrobus* has been attributed to the same plant as *Czekanowskia* and *Solenites*. The leaves are borne on short shoots and may be either simple (*Solenites*) or finely and dichotomously branched (*Czekanowskia*). The microsporangiate organ *Ixostrobus* has been linked with *Czekanowskia* at some localities (Krassilov, 1970), but in the Middle Jurassic flora of Yorkshire the evidence for linking *Leptostrobus cancer* with *Ixostrobus whitbiensis* is weak, and *Ixostrobus* may be attributed equally well to *Desmiophyllum gramineus* (Harris et al., 1974).

*Leptostrobus* is not well understood, but some inferences concerning its systematic relationships are possible with reference to the cladogram. The presence of scale leaves at the base of the "capsule"-bearing axis suggests that it is morphologically an axial structure. The "capsules" therefore may be homologous to "cupulate" megasporophylls. The valves of the "capsule" could be interpreted either as a single bivalved "cupule" or as a pair of closely associated "cupules" (character 9.19). However, *Leptostrobus* has a resistant megaspore membrane and has several seeds in each cupule (i.e., lacks characters 9.20, 9.22). Its position in the cladogram therefore could be hypothesized as above the level of *Callistophyton* and peltasperms but below that of Gnetales, Bennettitales, and *Pentoxylon*. This hypothesis, however, may conflict with evidence from leaf morphology (character 9.11) and further characters are needed to pursue the issue.



#### PROBLEMS AND POSSIBILITIES FOR FUTURE RESEARCH

The analysis presented in this paper is open to criticisms of various kinds. However, criticisms of the lack of direct paleobotanical evidence of morphological transitions and the supposed invalidation of the results by pernicious homoplasy are straightforwardly rejected.

The view that "direct" paleontological evidence is the final arbiter in elucidating phylogeny, and therefore in determining phylogenetic relationships, is entrenched in much botanical literature, but the kind of decisive paleontological evidence that might be required or expected is rarely elaborated. Finely graded series of intermediates that can be "read directly from the rocks" are not a common feature of the paleontological record (Crane, 1984), and it is naive to expect the simple description of further fossils to miraculously reveal plant phylogeny. As in other areas of paleontology, paleobotanists will always be faced with a problem of determining phylogenetic relationships between superficially dissimilar organisms without an unequivocal series of intermediates. The problem of determining plant phylogeny is therefore to produce a classification that reflects phylogenetic relationships. To accomplish this effectively requires an explicit method of classification that has a straightforward evolutionary interpretation.

The second common criticism, that homoplasy (parallelism, convergence, and reversal) is so pervasive that the character patterns revealed by phylogenetic analysis are meaningless, is frequently linked to functional arguments that invoke the influence of strong selective pressures. In plants there is certainly considerable homoplasy (Fig. 22). Perhaps this is to be expected in dominantly modular organisms with highly variable genetic mechanisms and the potential for extreme phenotypic plasticity. However, either character patterns are completely meaningless and any attempt to clarify plant phylogeny is abandoned; or the problem becomes how may homoplasy be recognized particularly in cases where the normal criteria of structural, positional, and developmental similarity are fulfilled? Homology may only be differentiated from homoplasy by reference to other characters (Fig. 22). The similar habit of some Euphorbiaceae and Cactaceae is interpreted as convergence because of different relationships that floral characters and other features indicate. The fact that homoplasy

can be assessed only in this way leads logically to a search for the simplest nested pattern for explaining the distribution of all features.

More serious, in my view, are problems that involve the analysis of characters on which the cladogram is based. A brief attempt has been made to justify the monophyly of Bennettitales, cycads, conifers, glossopterids, Gnetales, and angiosperms in order to simplify the analysis, but the assumptions involved need to be tested as a more detailed understanding is developed of relationships within these groups. Similarly, generalizations concerning groups of fossil plants such as the medullosans may be shown to be unjustified if future work demonstrates that they are heterogeneous fossil taxa (Beck, 1981: 193). Assumptions about unknown characters in certain fossil plants are also problematic. These were kept to a minimum and are explicitly identified in the character tables. The basis for many is explained in the text, but others were merely scored as plesiomorphic to minimize their influence on patterns of relationships. The necessity for these assumptions highlights the relatively poor understanding of many fossil taxa as whole plants. Current knowledge is highly uneven, and it is clear that there is as much need to understand our present fossils better as to discover new fossil taxa (Harris et al., 1974: 85).

Recognition of these problems has highlighted specific questions that need to be addressed by future neontological and paleobotanical research. Those particularly important to resolving the relationships between "Mesozoic seed ferns," Bennettitales, Gnetales, and angiosperms are:

a) Clarification of integument ontogeny, anatomy, and vasculature in peltasperms, *Caytonia*, corystosperms, and particularly in glossopterids.

b) Clarification of the manner in which microsporophylls and megasporophylls were borne in peltasperms, glossopterids, *Caytonia*, and corystosperms. Reexamination of the corystosperms would be particularly useful to reveal details of megasporophyll construction and the morphology of ovules and cupules. Further study of silicified glossopterid material should also clarify the relationship between the megasporophyll and "subtending bract."

c) Comparison of the outer seed covering ("cupule") of *Vardekloeftia* with the outer integumentary layer of anatomically preserved Bennettitales and *Pentoxylon*.

d) Comparison of the anatomy and biology of bennettitalean, gnetalean, and angiosperm ovules,



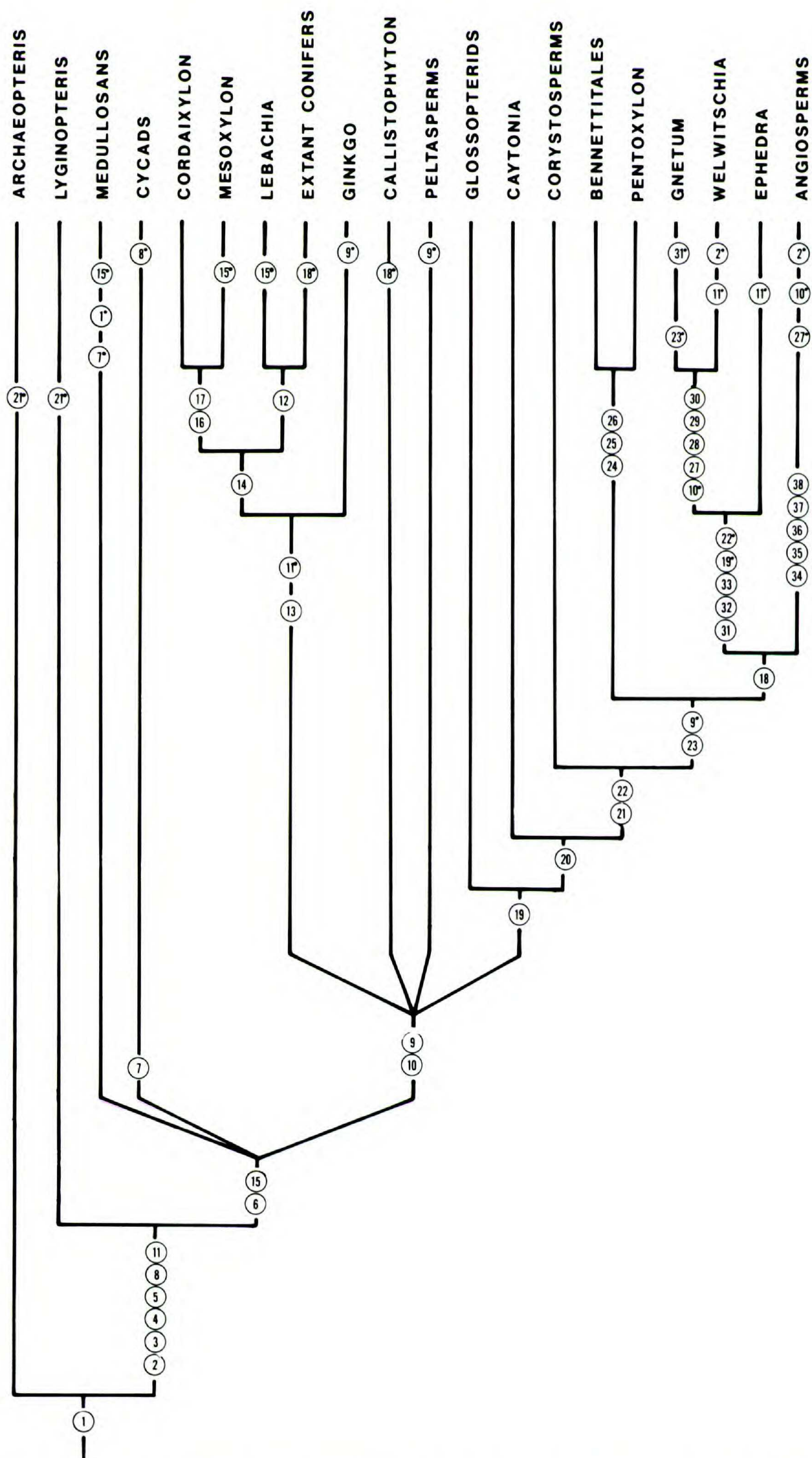


FIGURE 22. Relationships between major groups of seed plants. Strict consensus tree derived from ten equally parsimonious cladograms constructed from version two of the data matrix. In this analysis the “cupules” of



and detailed evaluation of the evidence for platyspermy in these taxa, especially angiosperms.

e) Comparative study of “seed cuticles,” including the megaspore membrane in living and fossil plants using modern techniques (Hill & Crane, 1982).

f) Comparative study of pollen wall stratification in “Mesozoic seed ferns,” *Pentoxylon*, and Bennettitales.

g) Attempts to identify the plants producing dispersed Mesozoic “*Ephedra*-like” pollen.

Further difficulties with the analysis are the use of “reduction” or “loss” characters, e.g., lack of archegonia (character 9.29) and the relatively small number of characters available. It is a tenuous position to regard two taxa as identical with respect to a condition that cannot actually be observed, but such characters may provide useful synapomorphies if they can be correlated with other features.

Similarly, examination of additional features clearly is desirable but is constrained in part by lack of comparative information for seed plants as a whole, including living representatives. In many cases characters that have been surveyed in detail in one group of seed plants have been examined only cursorily, or not at all, in others. Most botanical comparative studies have concentrated on taxa within seed plants and, as a result, have tended to reinforce their apparent differences.

### CONCLUSIONS

The approach outlined in this paper does not differ fundamentally from approaches previously used in paleobotany to interpret early land plant evolution (Banks, 1975; Chaloner, 1970b), early angiosperm evolution (Doyle, 1978; Doyle & Hickey, 1976), and studies of the major patterns of angiosperm leaf architecture (Hickey & Wolfe, 1975). It differs only in being relatively explicit and in attempting to define a highly resolved hierarchy of relationships. In the context of seed plants it has attempted, for the first time, to provide a detailed scheme of relationships accounting for both neontological and paleontological data.

The characters considered support a monophyletic origin of seed plants. *Lyginopteris* is placed as the sister taxon to all other seed plants. Flattened seeds and saccate pollen together define a major group of seed plants (“platysperms”) including conifers, cordaites, *Ginkgo*, *Callistophyton*, peltasperms, glossopterids, *Caytonia*, and corystosperms. If the outer integument of bennettitalean, *Pentoxylon*, and angiosperm bitegmic ovules is homologous to the “cupule” of glossopterids, *Caytonia*, and corystosperms then these groups plus the Gnetales form a clade of “higher” “platysperms” within the “platysperm” group. Such an interpretation would reconcile the widely accepted view that “Mesozoic seed ferns” are highly relevant to the problem of angiosperm origins with the idea proposed at the beginning of this century that Bennettitales and Gnetales are closely related to flowering plants. If this is accepted the corystosperms are the sister group to the “higher platysperms.” The Bennettitales and *Pentoxylon* are resolved as sister taxa and together form the sister group of angiosperms plus the Gnetales. The Gnetales are monophyletic and the sister group of flowering plants.

This pattern of relationships precludes any close phylogenetic connection between cycads and Bennettitales and emphasizes the heterogeneity of the seed ferns as currently recognized. The seed ferns include taxa of very diverse relationships. The current concept of the pteridosperms is therefore phylogenetically meaningless and confuses discussions of phylogenetic relationships.

The interpretation of seed plant relationships presented in this paper (particularly cladogram 2) is in broad agreement with the first stratigraphic appearance of the various taxa. It suggests that increased understanding of Triassic Bennettitales, Gnetales, and corystosperms will be of major interest in further elucidating the phylogenetic relationships of flowering plants. It may also suggest a substantially earlier time of origin for the flowering plant clade than is currently envisaged.

A Triassic or Jurassic origin would not conflict with the hypotheses of angiosperm diversifica-

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Bennettitales and *Pentoxylon* were coded as homologous to the “cupules” of glossopterids, *Caytonia*, corystosperms, and angiosperms. Bennettitales and *Pentoxylon* were coded as apomorphic for characters 9.19, 9.22, and 9.25. Total characters 38, character state transitions 62. A dot next to the number indicates homoplasy.



tion proposed by Doyle and Hickey (1976) and would suggest a pattern of evolutionary history for flowering plants similar to that of mammals with an early Mesozoic origin followed by low diversity and a delayed radiation. There are still, however, no unequivocal pre-Cretaceous angiosperm records, although there is an abundance of enigmatic Mesozoic plants about which we know almost nothing. Among these problematica that show angiosperm-like characters are the following: *Furcula* (Harris, 1932a), *Marcouia* (Ash, 1972a), *Scoresbya* (Kräusel & Schaaerschmidt, 1968), and *Phyllites* (Seward, 1904). In palynology, the reticulate, columellate, monosulcate grains reported by Cornet from the Upper Triassic–Lower Jurassic Newark Supergroup of the eastern United States are very similar to those of angiosperms (Doyle, 1978).

The principal difficulty with the phylogenetic analysis presented in this paper is the problem of dealing with missing characters in many potentially critical fossil plants. However, recognition of important areas of ignorance is of value in providing a focus for future paleobotanical work with phylogenetic objectives. The tests of the hypotheses presented here will come from future paleobotanical discoveries and the careful application of additional characters from neobotanical and paleobotanical research.

## LITERATURE CITED

- ALVIN, K. L. & W. G. CHALONER. 1970. Parallel evolution in leaf venation: an alternative view of angiosperm origins. *Nature* 226: 662–663.
- ANDERSON, J. M. & H. M. ANDERSON. 1983. Paleoflora of Southern Africa. Molteno Formation (Triassic). Volume 1. Part 1. Introduction. Part 2. *Dicroidium*. A. A. Balkema, Rotterdam.
- ANDREWS, H. N. 1961. *Studies in Paleobotany*. Wiley and Sons, New York.
- . 1963. Early seed plants. *Science* 142: 925–931.
- & C. J. FELIX. 1952. The gametophyte of *Cardiocarpus spinatus* Graham. *Ann. Missouri Bot. Gard.* 39: 127–135.
- ANTEVS, E. 1914. *Lepidopteris ottonis* (Göpp.) Schimp. and *Antholithus zeilleri* Nath. *Kunigl. Svenska Vetenskapsakad. Handl.* 51(7): 1–18.
- ARBER, E. A. N. & J. PARKIN. 1907. On the origin of angiosperms. *J. Linn. Soc., Bot.* 38: 29–80.
- & ———. 1908. Studies on the evolution of angiosperms. The relationship of the angiosperms to the Gnetales. *Ann. Bot. (London)* 22: 489–515.
- ARCHANGELSKY, S. 1963. A new Mesozoic flora from Ticó, Santa Cruz Province, Argentina. *Bull. Brit. Mus. (Nat. Hist.), Geol.* 8: 47–92.
- . 1965. Fossil Ginkgoales from the Ticó Flora, Santa Cruz Province, Argentina. *Bull. Brit. Mus. (Nat. Hist.), Geol.* 10: 119–137.
- . 1968. Studies on Triassic fossil plants from Argentina. IV. The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. *Palaeontology* 11: 500–512.
- & D. W. BRETT. 1961. Studies on Triassic fossil plants from Argentina, I. *Rhexoxylon* from the Ischigualasto Formation. *Philos. Trans.* 244: 1–19.
- & R. WAGNER. 1983. *Glossopteris anatolica* sp. nov. from uppermost Permian strata in south-east Turkey. *Brit. Mus. (Nat. Hist.), Geol.* 37: 81–91.
- ARNOLD, C. A. 1948. Classification of gymnosperms from the viewpoint of paleobotany. *Bot. Gaz. (Crawfordsville)* 110: 2–12.
- . 1953. Origin and relationships of the cycads. *Phytomorphology* 3: 51–65.
- ASH, S. R. 1972a. *Marcouia*, gen. nov., a problematical plant from the late Triassic of the southwestern U.S.A. *Palaeontology* 15: 423–429.
- . 1972b. Late Triassic plants from the Chinle Formation in northeastern Arizona. *Palaeontology* 15: 598–618.
- . 1975. *Zamites powelli* and its distribution in North America. *Palaeontographica, Abt. B, Paläophytol.* 149: 139–152.
- . 1976. The systematic position of *Eoginkgoites*. *Amer. J. Bot.* 63: 1327–1331.
- . 1977. An unusual bennettitalean leaf from the Upper Triassic of the southwestern United States. *Palaeontology* 20: 641–649.
- . 1982. Occurrence of the controversial plant fossil *Sanmiguelia* cf. *S. lewisi* Brown in the Upper Triassic of Utah. *J. Paleontol.* 56: 751–754.
- AUDRAN, J. C. & E. MASURE. 1977. Contribution à la connaissance de la composition des sporodermes chez les Cycadales (Prespermaphytes). Etude en microscopie électronique à transmission (M.E.T.) et à balayage (M.E.B.). *Palaeontographica, Abt. B, Paläophytol.* 162: 115–158.
- BAILEY, I. W. 1944. The development of vessels in angiosperms and its significance in morphological research. *Amer. J. Bot.* 31: 421–428.
- & B. G. L. SWAMY. 1951. The conduplicate carpel of dicotyledons and its initial trends of specialization. *Amer. J. Bot.* 38: 373–379.
- BANKS, H. P. 1975. Reclassification of Psilophyta. *Taxon* 24: 401–413.
- BARANOVA, M. 1972. Systematic anatomy of the leaf epidermis in the Magnoliaceae and some related families. *Taxon* 21: 447–469.
- BASINGER, J. F. & D. L. DILCHER. 1984. Ancient bisexual flowers. *Science* 224: 511–513.
- , G. W. ROTHWELL & W. N. STEWART. 1974. Cauline vasculature and leaf trace production in medullosan pteridosperms. *Amer. J. Bot.* 61: 1002–1015.
- BECK, C. B. 1960. Connection between *Archaeopteris* and *Callixylon*. *Science* 131: 1524–1525.
- . 1970. The appearance of gymnosperm structure. *Biol. Rev. Cambridge Philos. Soc.* 45: 353–377.
- . 1976. Origin and early evolution of angiosperms: a perspective. Pp. 1–10 in C. B. Beck (ed-



- itor), Origin and Early Evolution of Angiosperms. Columbia Univ. Press, New York.
- . 1981. *Archaeopteris* and its role in vascular plant evolution. Pp. 193–230 in K. J. Niklas (editor), *Paleobotany, Paleoecology and Evolution*. Praeger, New York.
- , R. SCHMID & G. W. ROTHWELL. 1982. Stelar morphology and the primary vascular system of seed plants. *Bot. Rev. (Lancaster)* 48: 691–815.
- BECKER, H. F. 1972. *Sanmiguelia*, an enigma compounded. *Palaeontographica, Abt. B, Paläophytol.* 138: 181–185.
- BENSON, M. 1904. *Telangium scotti*, a new species of *Telangium (Calymmatotheca)* showing structure. *Ann. Bot. (London)* 18: 161–177.
- . 1908. On the contents of the pollen chamber of a specimen of *Lagenostoma ovoides*. *Bot. Gaz. (Crawfordsville)* 45: 409–412.
- . 1912. *Cordaites felicis* sp. nov., a cordaitalean leaf from the lower coal measures of England. *Ann. Bot. (London)* 26: 201–207.
- BERRIDGE, E. M. 1911. On some points of resemblance between gnetalean and bennettian seeds. *New Phytol.* 10: 140–144.
- BESSEY, C. E. 1897. Phylogeny and taxonomy of the angiosperms. *Bot. Gaz. (Crawfordsville)* 24: 145–178.
- . 1915. The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* 2: 109–164.
- BIERHORST, D. W. 1958. The tracheary elements of *Equisetum* with observations on the ontogeny of the internodal xylem. *Bull. Torrey Bot. Club* 85: 416–433.
- . 1960. Observations on tracheary elements. *Phytomorphology* 10: 249–305.
- . 1971. *Morphology of Vascular Plants*. Macmillan, New York.
- BIGELOW, R. S. 1956. Monophyletic classification and evolution. *Syst. Zool.* 5: 145–146.
- BLISS, M. 1921. The vessel in seed plants. *Bot. Gaz. (Crawfordsville)* 71: 314–326.
- BOLD, H. C. 1973. *Morphology of Plants*, 3rd edition. Harper and Row, New York.
- BONAMO, P. M. 1977. *Rellimia thomsonii* (Progymnospermopsida) from the Middle Devonian of New York State. *Amer. J. Bot.* 64: 1272–1285.
- & H. P. BANKS. 1967. *Tetraxylopteris schmidtii*: its fertile parts and its relationships within the Aneurophytales. *Amer. J. Bot.* 54: 755–768.
- BOR, J. 1978. A note on anatropy versus orthotropy. *Phytomorphology* 28: 219–224.
- BOSE, M. N. 1953. *Bucklandia sahnii* sp. nov. from the Jurassic of the Rajmahal Hills, Bihar. *Palaeobotanist* 2: 41–49.
- . 1967. *Weltrichia singhii* n. sp. from the Rajmahal Hills, Bihar. *Curr. Sci.* 36(2): 48–49.
- . 1968. A new species of *Williamsonia* from the Rajmahal Hills, India. *J. Linn. Soc., Bot.* 61: 121–127.
- , P. K. PAL & T. M. HARRIS. In press. The *Pentoxylon* plant. *Philos. Trans.*
- BREMER, K. & H. E. WANNTORP. 1981. The cladistic approach to plant classification. In V. A. Funk & D. R. Brooks (editors), *Advances in Cladistics*. Proceedings of the First Meeting of the Willi Hennig Society. New York Botanical Garden, New York.
- BRENNER, G. J. 1963. The spores and pollen of the Potomac Group of Maryland. *Bull. Maryland Dept. Geol. Mines Water Resources* 27: 1–215.
- . 1967. The gymnospermous affinity of *Eucoronioidites* Erdtman 1948. *Rev. Palaeobot. Palynol.* 5: 123–127.
- . 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. Pp. 23–47 in C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- . 1984. Late Hauterivian angiosperm pollen from the Helez Formation, Israel. 6th Int. Palynol. Conf., Calgary 1984: 15. [Abstract.]
- BUCHHOLZ, J. T. 1934. The classification of Coniferales. *Trans. Illinois State Acad. Sci.* 25: 112–113.
- & N. E. GRAY. 1948. A taxonomic revision of *Podocarpus*. I. The sections of the genus and their subdivisions with special reference to leaf anatomy. *J. Arnold Arbor.* 29: 49–63.
- BURGER, W. C. 1977. The Piperales and the Monocots, alternate hypotheses for the origin of monocotyledonous flowers. *Bot. Rev. (Lancaster)* 43: 345–393.
- CHALONER, W. G. 1970a. The evolution of miospore polarity. *Geosci. Man* 1: 47–56.
- . 1970b. The rise of the first land plants. *Biol. Rev. Cambridge Philos. Soc.* 45: 353–377.
- & J. M. PETTITT. 1964. A seed megaspore from the Devonian of Canada. *Palaeontology* 7: 29–36.
- , A. J. HILL & W. S. LACEY. 1977. First Devonian platyspermic seed and its implications in gymnosperm evolution. *Nature* 165: 233–235.
- CHAMBERLAIN, C. J. 1935. *Gymnosperms, Structure and Evolution*. Univ. of Chicago Press, Chicago.
- CHRISTIANSEN, H. 1969. On the pollen grain and the fertilization mechanism of *Pseudotsuga mensesii* (Mirbel) Franco var. *viridis* Schwer. *Silvae Genet.* 18: 97–104.
- COULTER, J. M. & C. J. CHAMBERLAIN. 1917. *Morphology of Gymnosperms*. Univ. of Chicago Press, Chicago.
- COUPER, R. A. 1956. Evidence for a possible gymnospermous affinity for *Tricolpites troedssonii* Erdtman. *New Phytol.* 55: 280–285.
- . 1958. British Mesozoic microspores and pollen grains, a systematic and stratigraphic study. *Palaeontographica, Abt. B, Paläophytol.* 103: 75–179.
- CRANE, P. R. 1984. Misplaced pessimism and misguided optimism: a reply to Mabberley. *Taxon* 33: 79–82.
- & D. L. DILCHER. 1984 [1985]. *Lesqueria*: an early angiosperm fruiting axis from the mid-Cretaceous. *Ann. Missouri Bot. Gard.* 71: 384–402.
- & C. R. HILL. In press. Cladistic and paleobotanical approaches to plant phylogeny. In H. N. Hoeningwald (editor), *Biological Metaphor and Cladistic Representation Outside of Biology*. Univ. of Pennsylvania Press, Philadelphia.
- CREPET, W. L. 1972. Investigations of North American cycadeoids: pollination mechanisms in *Cycadeoidea*. *Amer. J. Bot.* 59: 1048–1056.



- . 1974. Investigations of North American Cycadeoids: the reproductive biology of *Cycadeoidea*. *Palaeontographica*, Abt. B, Paläophytol. 148: 144–169.
- & T. DELEVORYAS. 1972. Investigations of North American cycadeoids: early ovule ontogeny. *Amer. J. Bot.* 59: 209–215.
- CRIDLAND, A. A. & J. E. MORRIS. 1960. *Spermopteris*, a new genus of pteridosperms from the Upper Pennsylvanian Series of Kansas. *Amer. J. Bot.* 47: 855–859.
- CROIZAT, L. 1960. *Principia Botanica*, 1 and 2. Croizat, Caracas.
- CRONQUIST, A. 1968. *The Evolution and Classification of Flowering Plants*. Houghton Mifflin, New York.
- . 1981. *An Integrated System of Classification of Flowering Plants*. Columbia Univ. Press, New York.
- , A. TAKHTAJAN & W. ZIMMERMANN. 1966. On the higher taxa of Embryobionta. *Taxon* 15: 129–134.
- DAGHLIAN, C. P. & T. N. TAYLOR. 1979. A new structurally preserved Pennsylvanian cordaitalean pollen organ. *Amer. J. Bot.* 66: 290–300.
- DALLIMORE, W. & A. B. JACKSON. 1948. *A Handbook of Coniferae, Including Ginkgoaceae*. Arnold, London.
- DAVIS, P. H. & V. H. HEYWOOD. 1973. *Principles of Angiosperm Taxonomy*. R. E. Krieger, New York.
- DELEVORYAS, T. 1955. The Medullosae—structure and relationships. *Palaeontographica*, Abt. B, Paläophytol. 97: 114–167.
- . 1959. Investigations of North American cycadeoids: *Monanthesia*. *Amer. J. Bot.* 46: 657–666.
- . 1963. Investigations of North American cycadeoids: cones of *Cycadeoidea*. *Amer. J. Bot.* 50: 45–52.
- . 1968. Some aspects of cycadeoid evolution. *J. Linn. Soc., Bot.* 61: 137–146.
- . 1969. Glossopterid leaves from the Middle Jurassic of Oaxaca, Mexico. *Science* 165: 895–896.
- . 1975. Mesozoic cycadophytes. Pp. 173–191 in K. S. W. Campbell (editor), *Gondwana Geology, Papers presented at the Third Gondwana Symposium, Canberra, Australia*. Australian National Univ. Press, Canberra.
- & R. C. HOPE. 1976. More evidence for a slender growth habit in Mesozoic cycadophytes. *Rev. Palaeobot. Palynol.* 21: 93–100.
- & T. N. TAYLOR. 1969. A probable pteridosperm with eremopterid foliage from the Allegheny Group of northern Pennsylvania. *Postilla* 133: 1–14.
- DELUCA, P., A. MORETTI, S. SABATO & G. SINISCALO GIGLIANO. 1980. The ubiquity of cyasin in cycads. *Phytochemistry* 19: 2230–2231.
- DENNIS, R. L. & D. E. EGGERT. 1978. *Parasporotheca*, gen. nov., and its bearing on the interpretation of the morphology of permineralized medullosan pollen organs. *Bot. Gaz. (Crawfordsville)* 139: 117–139.
- DICKISON, W. C. 1975 [1976]. The bases of angiosperm phylogeny: vegetative anatomy. *Ann. Missouri Bot. Gard.* 62: 590–620.
- DILCHER, D. L. 1979. Early angiosperm reproduction: an introductory report. *Rev. Palaeobot. Palynol.* 27: 291–328.
- & P. R. CRANE. 1984 [1985]. *Archaeanthus*: an early angiosperm from the Cenomanian of the western interior of North America. *Ann. Missouri Bot. Gard.* 71: 351–383.
- DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. *J. Arnold Arbor.* 50: 1–35.
- . 1973. The monocotyledons: their evolution and comparative biology. V. Fossil evidence on the early evolution of the monocotyledons. *Quart. Rev. Biol.* 48: 399–413.
- . 1978. Origin of angiosperms. *Annual Rev. Ecol. Syst.* 9: 365–392.
- & L. J. HICKEY. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139–206 in C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- , M. VAN CAMPO & B. LUGARDON. 1975. Observations on exine structure of *Eucommiidites* and Lower Cretaceous angiosperm pollen. *Pollen & Spores* 17: 429–486.
- DRINNAN, A. N. & T. C. CHAMBERS. 1985. A reassessment of *Taeniopteris daintreei* from the Victorian Early Cretaceous: a member of the Pentoxylales and a significant Gondwanaland plant. *Austral. J. Bot.* 33: 89–100.
- EAMES, A. J. 1952. Relationships of the Ephedrales. *Phytomorphology* 2: 79–100.
- . 1961. *Morphology of the Angiosperms*. McGraw Hill, New York.
- ECKENWALDER, J. E. 1976a. Reevaluation of Cupressaceae and Taxodiaceae: a proposed merger. *Madroño* 23: 237–256.
- . 1976b. Comments on “A new classification of the conifers.” *Taxon* 25: 337–339.
- EDWARDS, W. N. 1929. The Jurassic flora of Sardinia. *Ann. Mag. Nat. Hist.* 4: 385–394.
- EHRENDORFER, F. 1971. *Systematik und Evolution: Spermatophyta, Samenpflanzen*. Lehrbuch der Botanik für Hochschulen. G. Fisher, Stuttgart.
- . 1976. Evolutionary Significance of Chromosomal Differentiation Patterns in Gymnosperms and Primitive Angiosperms. Columbia Univ. Press, New York.
- ELDRIDGE, N. & J. CRACRAFT. 1980. *Phylogenetic Patterns and the Evolutionary Process*. Columbia Univ. Press, New York.
- EMBERGER, L. 1954. Sur les Ginkgoales et quelques rapprochements avec d'autres groupes systématiques. *Svensk Bot. Tidskr.* 48: 361–367.
- ENGLER, A. 1897. Principien der systematischen Anordnung, insbesondere der Angiospermen. In A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien*. W. Engelmann, Leipzig.
- ERDTMAN, G. 1948. Did dicotyledonous plants exist in early Jurassic times? *Förh. Geol. Fören Stockholm* 70: 265–271.
- . 1957. Pollen and Spore Morphology/Plant Taxonomy. Gymnospermae, Pteridophyta, Bryo-



- phyta (Illustrations). Almquist and Wiksell, New York.
- . 1965. Pollen and Spore Morphology/Plant Taxonomy. Gymnospermae, Bryophyta (text). Almquist and Wiksell, New York.
- FARRIS, J. S. 1982. Outgroups and parsimony. *Syst. Zool.* 31: 328–334.
- FLORIN, R. 1936. On the structure of the pollen grains in the Cordaitales. *Svensk Bot. Tidskr.* 30: 624–651.
- . 1948. On the morphology and relationships of the Taxaceae. *Bot. Gaz. (Crawfordsville)* 110: 31–39.
- . 1951. Evolution in *Cordaite*s and conifers. *Acta Horti Berg.* 15: 285–388.
- . 1954. The female reproductive organs of conifers and taxads. *Biol. Rev. Cambridge Philos. Soc.* 29: 367–389.
- . 1955. The systematics of the gymnosperms. Pp. 323–403 in *A Century of Progress in the Natural Sciences*. California Academy of Science, San Francisco.
- FOSTER, A. S. & E. M. GIFFORD. 1974. Comparative Morphology of Vascular Plants, 2nd edition. W. H. Freeman, San Francisco.
- GAUSSEN, H. 1946. Les Gymnospermes, actuelles et fossiles. *Trav. Lab. Forest. Toulouse*, Tome 2, Etud. Dendrol., Sect. 1, 1 (3,5): 1–26.
- GIBBS, R. D. 1958. The Maule reaction, lignins and the relationships between woody plants. In K. V. Thimann (editor), *The Physiology of Forest Trees*. Ronald, New York.
- GIFFORD, E. M. & G. E. CORSON. 1971. The shoot apex in seed plants. *Bot. Rev. (Lancaster)* 37: 143–229.
- GILLESPIE, W. H., G. W. ROTHWELL & S. E. SCHECKLER. 1981. The earliest seeds. *Nature* 293: 462–464.
- GOOD, C. W. & T. N. TAYLOR. 1970. On the structure of *Cordaite felicit*s Benson from the Lower Pennsylvanian of North America. *Palaeontology* 13: 29–39.
- GOTTLIEB, O. R. & K. KUBITZKI. 1984. Chemosystematics of Gnetatae and the chemical evolution of seed plants. *Pl. Med.* 1984: 365–458.
- GOULD, R. E. 1975. A preliminary report on petrified axes of *Vertebraria* from the Permian of eastern Australia. Pp. 109–115 in K. S. W. Campbell (editor), *Gondwana Geology*, Papers presented at the Third Gondwana Symposium, Canberra, Australia. Australian National Univ. Press, Canberra.
- & T. DELEVORYAS. 1977. The biology of *Glossopteris*: evidence from petrified seed-bearing and pollen-bearing organs. *Alcheringa* 1: 387–399.
- GRAHAM, G. O. 1935. Pennsylvanian flora of Illinois as revealed in coal balls. II. *Bot. Gaz. (Crawfordsville)* 97: 156–168.
- GREGUSS, P. 1968. Xylotomy of the Living Cycads, With a Description of Their Leaves and Epidermis. Akadémiai Kiadó, Budapest.
- . 1972. Xylotomy of the Living Conifers. Akadémiai Kiadó, Budapest.
- GROVE, G. G. & G. W. ROTHWELL. 1980. *Mitrospermum vinculum* sp. nov., a cardiocarpalean ovule from the Upper Pennsylvanian of Ohio. *Amer. J. Bot.* 67: 1051–1058.
- HALLE, T. G. 1929. Some seed-bearing pteridosperms from the Permian of China. *Kungl. Svenska Vetenskapsakad. Handl. Ser. 3*, 6(8): 1–24.
- HAMER, J. 1984. A small *Medullosa* from the Appalachian Basin. *Amer. J. Bot.* 71: 114. [Abstract.]
- HARMS, V. & G. A. LEISMAN. 1961. The anatomy and morphology of certain *Cordaite*s leaves. *J. Paleontol.* 35: 1041–1064.
- HARRIS, T. M. 1926. The Rhaetic Flora of Scoresby Sound East Greenland. *Meddel. Grønland* 68: 45–148.
- . 1932a. The fossil flora of Scoresby Sound East Greenland. Part 2: description of seed plants *incertae sedis* together with a discussion of certain cycadophyte cuticles. *Meddel. Grønland* 85(3): 1–114.
- . 1932b. The fossil flora of Scoresby Sound East Greenland. Part 3: Caytoniales and Bennettitales. *Meddel. Grønland* 85(5): 1–133.
- . 1933. A new member of the Caytoniales. *New Phytol.* 32: 97–114.
- . 1937. The fossil flora of Scoresby Sound East Greenland. Part 5. Stratigraphic relations of the plant beds. *Meddel. Grønland* 112(2): 1–114.
- . 1940a. *Caytonia*. *Ann. Bot. (London) n.s.* 4: 713–734.
- . 1940b. On some Jurassic specimens of *Sagenopteris*. *Ann. Mag. Nat. Hist.* 16: 250–265.
- . 1941. *Caytonanthus*, the microsporophyll of *Caytonia*. *Ann. Bot. (London) n.s.* 5: 47–58.
- . 1944. A revision of *Williamsoniella*. *Philos. Trans.* 231: 313–328.
- . 1945. A coprolite of *Caytonia* pollen. *Ann. Mag. Nat. Hist.* 12: 357–378.
- . 1951a. The fructification of *Czekanowskia* and its allies. *Philos. Trans.* 235: 483–508.
- . 1951b. The relationships of the Caytoniales. *Phytomorphology* 1: 29–39.
- . 1954. Mesozoic seed cuticles. *Svensk Bot. Tidskr.* 48: 281–291.
- . 1958. The seed of *Caytonia*. *Palaeobotanist* 7: 93–106.
- . 1960. The origin of angiosperms. *Advancem. Sci.* 17: 207–213.
- . 1962. The occurrence of the fructification *Carnoconites* in New Zealand. *Trans. Roy. Soc. New Zealand, Geol.* 4: 17–27.
- . 1964. The Yorkshire Jurassic Flora. II. Caytoniales, Cycadales and Pteridosperms. British Museum (Natural History), London.
- . 1969. The Yorkshire Jurassic Flora. III. Bennettitales. British Museum (Natural History), London.
- . 1971. The stem of *Caytonia*. *Geophytology* 1: 23–29.
- . 1974. *Williamsoniella lignieri*: its pollen and the compression of spherical pollen grains. *Palaeontology* 17: 125–148.
- . 1976. The Mesozoic gymnosperms. *Rev. Palaeobot. Palynol.* 21: 119–134.
- . 1983a. The stem of *Pachypteris papillosa* (Thomas & Bose) Harris. *Bot. J. Linn. Soc.* 86: 149–159.
- . 1983b. Fossils from New Zealand ascribed to the *Pentoxylon* plant. *Phyta (D. D. Pant Comm. Vol.)*. Pp. 91–103.
- , W. MILLINGTON & J. MILLER. 1974. The



- Yorkshire Jurassic Flora, IV: Ginkgoales and Czekanowskiales. British Museum (Natural History), London.
- HENNIG, W. 1965. Phylogenetic systematics. *Annual Rev. Entomol.* 10: 97–116.
- . 1966. *Phylogenetic Systematics*. Univ. of Illinois Press, Urbana.
- HICKEY, L. J. & J. A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev. (Lancaster)* 43: 3–104.
- & J. A. WOLFE. 1975 [1976]. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Missouri Bot. Gard.* 62: 538–589.
- HILL, C. R. & P. R. CRANE. 1982. Evolutionary cladistics and the origin of angiosperms. Pp. 269–361 in K. A. Joysey & A. E. Friday (editors), *Problems of Phylogenetic Reconstruction*. Academic Press, New York.
- , D. T. MOORE, J. T. GREENSMITH & R. WILLIAMS. In press. Rediscovery of a historic *Williamsonia* (plant fossil) locality in North Yorkshire: the Middle Jurassic ironstone bed at Wrack Hills. *Proc. Yorkshire Geol. Soc.* 45.
- HILL, T. G. & E. DEFRAINE. 1909. On the seedling structure of gymnosperms, II. *Ann. Bot. (London)* 23: 189–227.
- HOLMES, W. B. K. & S. R. ASH. 1979. An early Triassic megafossil flora from the Lorne Basin, New South Wales. *Proc. Linn. Soc. New South Wales* 103: 47–70.
- HOSKINS, J. H. & A. T. CROSS. 1946. Studies in the Trigonocarpaceae. Part II. Taxonomic problems and a revision of the genus *Pachytesta*. *Amer. Midl. Naturalist* 36: 331–361.
- HUGHES, N. F. 1961. Further interpretation of *Eucommiidites* Erdtman 1948. *Palaeontology* 4: 292–299.
- . 1976. *Palaeobiology of Angiosperm Origins*. Cambridge Univ. Press, Cambridge.
- . 1977. Palaeo-succession of earliest angiosperm evolution. *Bot. Rev. (Lancaster)* 43: 3–104.
- JEFFREY, E. C. 1903. The comparative anatomy of the Coniferales. I. The genus *Sequoia*. *Mem. Boston Soc. Nat. Hist.* 5: 441–459.
- JOHNSON, M. A. 1951. The shoot apex in gymnosperms. *Phytomorphology* 1: 188–204.
- JONGMANS, W. J. 1930. On the fructification of *Sphenopteris hoeninghausi* and its relations with *Lyginodendron oldhamium* and *Crossotheca schatzlarensis*. *Geologisch Bureau voor het Nederlandsche Mijngedebied te Heerlen* 1929: 77–81.
- JUST, T. K. 1948. Gymnosperms and the origin of angiosperms. *Bot. Gaz. (Crawfordsville)* 110: 91–103.
- KENG, H. 1975. A new scheme of classification of the conifers. *Taxon* 24: 289–292.
- KERP, J. H. F. 1982. Aspects of Permian paleobotany and palynology II. On the presence of *Autunia milleryensis* (Renault) Krasser (Peltaspermeaceae) in the Lower Permian of the Nahe Area (F. G. R.) and its relationship to *Callipteris conferta* (Sternberg) Brongniart. *Acta Bot. Neerl.* 31: 417–427.
- . 1983. Aspects of Permian palaeobotany and palynology. 1. *Sobernheimia jonkeri* nov. gen., nov. sp., a new fossil plant of cycadalean affinity from the Waderner Grappe of Sobernheim. *Rev. Palaeobot. Palynol.* 38: 173–183.
- KIDSTON, R. 1906. On the microsporangia of the Pteridospermeae, with remarks on their relationship to existing groups. *Philos. Trans.* 198: 413–445.
- KNOLL, A. H. & G. W. ROTHWELL. 1981. Paleobotany: perspectives in 1980. *Paleobiology* 7: 7–35.
- KONIJNENBURG-VAN CITTERT, J. H. A. VAN. 1971. In situ gymnosperm pollen from the Middle Jurassic of Yorkshire. *Acta Bot. Neerl.* 20: 1–96.
- KOSANKE, R. 1969. Mississippian and Pennsylvanian palynology. Pp. 223–269 in R. H. Tschudy & R. A. Scott (editors), *Aspects of Palynology*. Wiley and Sons, New York.
- KRASSILOV, V. A. 1970. Approach to the classification of Mesozoic “Ginkgoalean” plants from Siberia. *Palaeobotanist* 18: 12–19.
- . 1973. Mesozoic plants and the problem of angiosperm ancestry. *Lethaia* 6: 163–178.
- . 1975. Dirhopalostachyaceae—a new family of proangiosperms and its bearing on the problem of angiosperm ancestry. *Palaeontographica, Abt. B, Paläophytol.* 153: 100–110.
- . 1977a. Contributions to the knowledge of the Caytoniales. *Rev. Palaeobot. Palynol.* 24: 155–178.
- . 1977b. The origin of angiosperms. *Bot. Rev. (Lancaster)* 43: 143–176.
- . 1984 [1985]. New paleobotanical data on origin and early evolution of angiospermy. *Ann. Missouri Bot. Gard.* 71: 577–592.
- & V. I. BURAGO. 1981. New interpretation of *Gaussia* (Vojnovskyales). *Rev. Palaeobot. Palynol.* 32: 227–237.
- , P. V. SHILIN & V. A. VACHRAMEEV. 1983. Cretaceous flowers from Kazakhstan. *Rev. Palaeobot. Palynol.* 40: 91–113.
- KRÄUSEL, R. 1948. *Sturiella langeri* nov. gen. nov. sp. eine Bennettitee aus der Trias von Lunz (Nieder-Österreich). *Senckenbergiana* 29: 141–149.
- . 1949. Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-Österreich. *Palaeontographica, Abt. B, Paläophytol.* 84: 35–78.
- & F. SCHAARSCHMIDT. 1966. Die Keuperflora von Neuwelt bei Basel. IV. Pterophyllen und Taeniopteriden. *Schweiz. Paläontol. Abh.* 84: 1–64.
- & ———. 1968. *Scoresbya* Harris (Dipteridaceae?) aus dem Unteren Jura von Sassendorf. *Palaeontographica, Abt. B, Paläophytol.* 123: 124–131.
- LACEY, W. S. 1976. Further observations on the Molteno Flora of Rhodesia. *Arnoldia* 7: 1–14.
- & R. C. LUCAS. 1981. The Triassic flora of Livingston Island, South Shetland Islands. *Brit. Antarc. Surv. Bull.* 53: 157–173.
- LECLERQ, S. & P. M. BONAMO. 1971. A study of the fructification of *Milleria (Protopteridium) thomsonii* Lang from the Middle Devonian of Belgium. *Palaeontographica, Abt. B, Paläophytol.* 136: 83–114.
- LEE, C. L. 1955. Fertilization in *Ginkgo biloba*. *Bot. Gaz. (Crawfordsville)* 117: 79–100.
- LEHMANN-BAERTS, M. 1967. Ovule gametophyte fe-



- melle et embryogenese chez *Ephedra distachya* L. Cellule 67: 57–87.
- LEISMAN, G. A. 1961. A new species of *Cardiocarpus* in Kansas coal balls. Trans. Kansas State Acad. Sci. 64: 117–122.
- LONG, A. G. 1944. On the prothallus of *Lagenostoma ovoides* Will. Ann. Bot. (London) n.s. 8: 105–117.
- . 1959. On the structure of "*Calymmatotheca kidstoni*" Calder (emended) and "*Genomosperma latens*" gen. et sp. nov. from the calciferous sandstone series of Berwickshire. Trans. Roy. Soc. Edinburgh 64: 29–44.
- . 1960. On the structure of "*Samaropsis scotica*" Calder (emended) and "*Euryostoma angulare*" gen. et sp. nov., petrified seeds from the calciferous sandstone series of Berwickshire. Trans. Roy. Soc. Edinburgh 64: 261–280.
- . 1966. Some Lower Carboniferous fructifications from Berwickshire, together with a theoretical account of the evolution of ovules, cupules and carpels. Trans. Roy. Soc. Edinburgh 66: 345–375.
- . 1975. Further observations on some Lower Carboniferous seeds and cupules. Trans. Roy. Soc. Edinburgh 69: 267–293.
- . 1977. Lower Carboniferous pteridosperm cupules and the origin of angiosperms. Trans. Roy. Soc. Edinburgh 70: 13–35.
- LUGARDON, B. & A. LETHOMAS. 1974. Sur la structure femilletée de la couche basale de l'ectexine chez diverses Annonacées. Compt. Rend. Hebd. Séances Acad. Sci., Ser. D, 279: 255–258.
- LUNDBLAD, A. B. 1948. On some *Caytonia*-like plant-remains from the coal mines of Bjuv in Scania (Rhaetic). Svensk Bot. Tidskr. 42: 84–86.
- . 1950. Studies in the Rhaeto-Liassic floras of Sweden. I. Pteridophyta, Pteridospermae, and Cycadophyta from the Mining District of NW Scania. Kungl. Svenska Vetenskapsakad. Handl., Ser. 4, 1(8): 1–81.
- MABBERLEY, D. J. 1984. The optimistic in pursuit of the unrecognisable: a note on the origin of angiosperms. Taxon 33: 77–79.
- MCLEAN, R. C. 1912. Two fossil prothalli from the Lower Coal Measures. New Phytol. 11: 305–318.
- MCLEAN, R. & M. EVANS. 1934. The Maule reaction and the systematic position of the Gnetales. Nature 134: 936–937.
- MAHESHWARI, P. & S. V. MEYEN. 1975. *Cladostrobus* and the systematics of cordaitalean leaves. Lethaia 8: 103–123.
- & V. VASIL. 1961. The stomata of *Gnetum*. Ann. Bot. (London) n.s. 25: 313–319.
- MAMAY, S. H. 1966. *Tinsleya*, a new genus of seed-bearing callipterid plants from the Permian of Texas. Profess. Pap. U.S. Geol. Surv. 523E: 1–15.
- . 1975. *Sandrewia*, n. gen., a problematical plant from the Lower Permian of Texas and Kansas. Rev. Palaeobot. Palynol. 20: 75–83.
- . 1976. Paleozoic origin of the cycads. Profess. Pap. U.S. Geol. Surv. 934: 1–48.
- . 1978. Vojnovskyales in the Lower Permian of North America. Palaeobotanist 25: 290–297.
- & A. D. WATT. 1971. An ovuliferous callipteroid plant from the Hermit Shale (Lower Permian) of the Grand Canyon, Arizona. Profess. Pap. U.S. Geol. Surv. 750C: 48–51.
- MAPES, G. & G. W. ROTHWELL. 1980. *Quaestora amplexa* gen. et sp. n., a structurally simple medullosan stem from the Upper Mississippian of Arkansas. Amer. J. Bot. 67: 636–647.
- & ———. 1984. Permineralized ovulate cones of *Lebachia* from the late Palaeozoic limestones of Kansas. Palaeontology 27: 69–94.
- MARTENS, P. 1971. Les gnétophytes. Handb. Pflanzenanat. 12(2): 1–295.
- & L. WATERKEYN. 1963. The shoot apical meristem of *Welwitschia mirabilis* Hooker. Phytomorphology 13: 359–363.
- MATTEN, L. C., T. I. FINE, W. R. TANNER & W. S. LACEY. 1984. The megagametophyte of *Hydrasperma tenuis* Long from the Upper Devonian of Ireland. Amer. J. Bot. 71: 1461–1464.
- MEEUSE, A. D. J. 1966. Fundamentals of Phytomorphology. Ronald Press, New York.
- MEHRA, P. N. 1950. Occurrence of hermaphrodite flowers and the development of female gametophyte in *Ephedra intermedia* Shrenk et Mey. Ann. Bot. (London) n.s. 14: 165–180.
- MELVILLE, R. 1962. A new theory of the angiosperm flower. I. The gynoeceum. Kew Bull. 16: 1–50.
- . 1963. A new theory of the angiosperm flower. II. The androeceum. Kew Bull. 17: 1–63.
- MELVIN, J. F. & C. M. STEWART. 1969. The chemical composition of the wood of *Gnetum gnemon*. Holzforshung 23: 51–56.
- MEYEN, S. V. 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. Bot. Rev. (Lancaster) 50: 1–111.
- MICKLE, J. E. & G. W. ROTHWELL. 1982. Permineralized *Alethopteris* from the Upper Pennsylvanian of Ohio and Illinois. J. Paleontol. 56: 392–402.
- MILLAY, M. A. & D. A. EGGERT. 1974. Microgametophyte development in the Paleozoic seed fern family Callistophytaceae. Amer. J. Bot. 61: 1067–1075.
- & T. N. TAYLOR. 1974. Morphological studies of Paleozoic saccate pollen. Palaeontographica, Abt. B, Paläophytol. 147: 75–99.
- & ———. 1976. Evolutionary trends in fossil gymnosperm pollen. Rev. Palaeobot. Palynol. 21: 65–91.
- , D. A. EGGERT & R. L. DENNIS. 1978. Morphology and ultrastructure of four Pennsylvanian prepollen types. Micropaleontology 24: 303–315.
- MILLER, C. N. 1982. Current status of Paleozoic and Mesozoic conifers. Rev. Palaeobot. Palynol. 37: 99–114.
- MILLER, J. M. & D. M. ROHR. 1982. A new species of *Spermopteris* from the Upper Permian (Gua-dalupian) Word Formation, Del Norte Mountains, Texas. Publ. Bot. Soc. Amer., Misc. Ser. 162: 62. [Abstract.]
- MISHLER, B. D. & S. P. CHURCHILL. 1984. A cladistic approach to the phylogeny of the "bryophytes." Brittonia 36: 406–424.
- MOGENSEN, H. L. 1978. Synergids of *Proboscidea louisianica* (Martineaceae) before fertilization. Phytomorphology 28: 114–122.



- MORETTI, A., S. SABATTO & G. SINISCALCO GIGLIANO. 1983. Taxonomic significance of methylazoxymethanol glycosides in the cycads. *Phytochemistry* 22: 115–117.
- MOUSSEL, B. 1978. Double fertilization in the genus *Ephedra*. *Phytomorphology* 28: 336–345.
- MUHAMMAD, A. F. & R. SATTler. 1982. Vessel structure of *Gnetum* and the origin of angiosperms. *Amer. J. Bot.* 69: 1004–1021.
- MULLER, J. 1970. Palynological evidence on the early differentiation of the angiosperms. *Biol. Rev. Cambridge Philos. Soc.* 45: 417–450.
- . 1981. Fossil pollen records of extant angiosperms. *Bot. Rev. (Lancaster)* 48: 1–142.
- . 1984 [1985]. Significance of fossil pollen for angiosperm history. *Ann. Missouri Bot. Gard.* 71: 419–443.
- NATHORST, A. G. 1909. Paläobotanische Mitteilungen, 8. Über *Williamsonia*, *Wielandia*, *Cycadocephalus* und *Weltrichia*. *Kungl. Svenska Vetenskapsakad. Handl.* 45(4): 1–38.
- NELSON, G. J. 1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's *Familles des Plantes* (1763–1764). *Syst. Zool.* 28: 1–21.
- NISHIO, K. 1959. Investigations with the Mäule reaction on plant tissues. I. *Bot. Mag. (Tokyo)* 72: 384–387.
- NORSTOG, K. 1977. The spermatozoid of *Zamia chigua* Seem. *Bot. Gaz. (Crawfordsville)* 138: 409–412.
- OESTRY-STIDD, L. L. & B. M. STIDD. 1976. Paracytic (syndetocheilic) stomata in Carboniferous seed ferns. *Science* 193: 156–157.
- OLIVER, F. W. & D. H. SCOTT. 1904. On the structure of the Paleozoic seed *Lagenostoma lomaxi* with a statement of the evidence on which it is referred to *Lyginodendron*. *Philos. Trans.* 197: 193–247.
- PANT, D. D. 1977a. The plant of *Glossopteris*. *J. Indian Bot. Soc.* 56: 1–23.
- . 1977b. Early conifers and conifer allies. *J. Indian Bot. Soc.* 56: 23–37.
- & N. BASU. 1973. *Pteruchus indicus* sp. nov. from the Triassic of Nidpur, India. *Palaeontographica, Abt. B, Paläophytol.* 144: 11–24.
- & ———. 1979. Some further fructifications from the Triassic of Nidpur, India. *Palaeontographica, Abt. B, Paläophytol.* 168: 129–146.
- & D. D. NAUTIYAL. 1960. Some seeds and sporangia of *Glossopteris* flora from Raniganj coalfield, India. *Palaeontographica, Abt. B, Paläophytol.* 107: 41–64.
- & ———. 1965. Seed bearing *Ottokaria*-like fructifications from India. *Nature* 207: 623–624.
- & ———. 1984. On the morphology and structure of *Ottokaria zeilleri* sp. nov., a female fructification of *Glossopteris*. *Palaeontographica, Abt. B, Paläophytol.* 193: 127–152.
- & R. S. SINGH. 1974. On the stem and attachment of *Glossopteris* and *Gangamopteris* leaves. Part II. Structural features. *Palaeontographica, Abt. B, Paläophytol.* 147: 42–73.
- PARENTI, L. R. 1980. A phylogenetic analysis of the land plants. *Biol. J. Linn. Soc.* 13: 225–242.
- . 1982. Cladistics and conventions. *Taxon* 31: 96–101.
- PATTERSON, C. 1982a. Morphological characters and homology. In K. A. Joysey & A. E. Friday (editors), *Problems of Phylogenetic Reconstruction*. Academic Press, New York.
- . 1982b. Classes and cladists or individuals and evolution. *Syst. Zool.* 31: 284–286.
- PEARSON, H. H. W. 1915. Notes on the morphology of certain structures concerned in reproduction in the genus *Gnetum*. *Trans. Linn. Soc. London, Bot.* 8: 311–332.
- . 1929. *Gnetales*. Cambridge Univ. Press, Cambridge.
- PETRIELLA, B. 1979. Sinopsis de las *Corystospermaceae* (*Corystospermales*, *Pteridospermophyta*) de Argentina. I. Hojas. *Ameghiniana* 16: 81–102.
- . 1980. Sinopsis de las *Corystospermaceae* (*Corystospermales*, *Pteridospermophyta*) de Argentina. II. Estructuras fertiles. *Ameghiniana* 17: 168–180.
- . 1981. Sistemática y vinculaciones de las *Corystospermaceae* H. Thomas. *Ameghiniana* 18: 221–234.
- . 1983. Sinopsis de las *Corystospermaceae* (*Corystospermales*, *Pteridospermophyta*) de la Argentina. III. Troncos y chrono-stratigrafía. *Ameghiniana* 20: 41–46.
- PETTITT, J. M. 1966. Exine structure in some fossil and Recent spores and pollen as revealed by light and electron microscopy. *Bull. Brit. Mus. (Nat. Hist.), Geol.* 13: 221–257.
- . 1969. Pteridophytic features in some Lower Carboniferous seed megaspores. *J. Linn. Soc., Bot.* 62: 233–239.
- . 1970. Heterospory and the origin of the seed. *Biol. Rev. Cambridge Philos. Soc.* 45: 401–415.
- & C. B. BECK. 1968. *Archaeosperma arnoldii*—a cupulate seed from the Upper Devonian of North America. *Contr. Mus. Paleontol. Univ. Michigan* 10: 139–154.
- PHILLIPS, T. L., H. N. ANDREWS & P. G. GENSEL. 1972. Two heterosporous species of *Archaeopteris* from the Upper Devonian of West Virginia. *Palaeontographica, Abt. B, Paläophytol.* 139: 47–71.
- PIGG, K. B. & G. W. ROTHWELL. 1983. *Chaloneria* gen. nov. heterosporous lycophytes from the Pennsylvanian of North America. *Bot. Gaz. (Crawfordsville)* 144: 132–147.
- PLATNICK, N. I. 1979. Philosophy and the transformation of cladistics. *Syst. Zool.* 28: 537–546.
- . 1982. Defining characters and evolutionary groups. *Syst. Zool.* 31: 282–284.
- RAMANUJAM, C. G. K., G. W. ROTHWELL & W. N. STEWART. 1974. Probable attachment of the *Doleriotheca* campanulum to a *Myeloxylon-Alethopteris* type frond. *Amer. J. Bot.* 61: 1057–1066.
- RAO, A. R. 1976. Problems in the Pentoxyleae. *Palaeobotanist* 25: 393–396.
- . 1981. The affinities of the Pentoxyleae. *Palaeobotanist* 28–29: 207–209.
- RAVEN, P. H. 1975 [1976]. The bases of angiosperm phylogeny: cytology. *Ann. Missouri Bot. Gard.* 62: 724–764.
- REIHMAN, M. A. & J. T. SCHABILION. 1978. Petrified neuropterid foliage from a Middle Pennsylvanian coal ball. *Amer. J. Bot.* 65: 834–844.
- RENDLE, A. B. 1925. The Classification of Flowering



- Plants. Volume 2. Dicotyledons. Cambridge Univ. Press, Cambridge.
- . 1930. The Classification of Flowering Plants. Volume 1. Gymnosperms and Monocotyledons, 2nd edition. Cambridge Univ. Press, Cambridge.
- RETALLACK, G. J. 1977. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa* 1: 247–277.
- & D. L. DILCHER. 1981. Arguments for a glossopterid ancestry of angiosperms. *Paleobiology* 7: 54–67.
- REYMANÓWNA, M. 1968. On seeds containing *Eucommiidites troedssonii* pollen from the Jurassic of Grojec, Poland. *J. Linn. Soc., Bot.* 61: 147–152.
- . 1973. The Jurassic flora from Grojec near Kraków in Poland. Part II. Caytoniales and anatomy of *Caytonia*. *Acta Palaeobot.* 14: 45–87.
- RIGGINS, R. & J. S. FARRIS. 1983. Cladistics and the roots of angiosperms. *Syst. Bot.* 8: 96–100.
- RODIN, R. J. & R. N. KAPIL. 1969. Comparative anatomy of the seed coats of *Gnetum* and their probable evolution. *Amer. J. Bot.* 56: 420–431.
- ROHLF, F. J. 1982. Consensus indices for comparing classifications. *Math. Biosci.* 59: 131–144.
- ROTHWELL, G. W. 1971. Ontogeny of the Paleozoic ovule *Callospermario pusillum*. *Amer. J. Bot.* 58: 706–715.
- . 1972. Evidence of pollen tubes in Paleozoic pteridosperms. *Science* 175: 772–774.
- . 1975. The Callistophytaceae (Pteridospermopsida): I. Vegetative structures. *Palaeontographica, Abt. B, Paläophytol.* 151: 171–196.
- . 1977. The primary vasculature of *Cordaianthus concinnus*. *Amer. J. Bot.* 64: 1235–1241.
- . 1980. The Callistophytaceae (Pteridospermopsida). II. Reproductive features. *Palaeontographica, Abt. B, Paläophytol.* 173: 85–106.
- . 1981. The Callistophytales (Pteridospermopsida): reproductively sophisticated Paleozoic gymnosperms. *Rev. Palaeobot. Palynol.* 32: 103–121.
- . 1982a. New interpretations of the earliest conifers. *Rev. Palaeobot. Palynol.* 37: 7–28.
- . 1982b. *Cordaianthus duquesnensis* sp. nov., anatomically preserved ovulate cones from the Upper Pennsylvanian of Ohio. *Amer. J. Bot.* 69: 239–247.
- & S. WARNER. 1982. A shrubby cordaitan from the Upper Pennsylvanian of the Appalachian Basin. *Publ. Bot. Soc. Amer., Misc. Ser.* 162: 63. [Abstract.]
- & ———. 1984. *Cordaioxylon dumusum* n. sp. (Cordaitales). I. Vegetative structures. *Bot. Gaz. (Crawfordsville)* 145: 275–291.
- SAHNI, B. 1932a. *Homoxylon rajmahalense* gen. et sp. nov., a fossil angiospermous wood devoid of vessels, from the Rajmahal Hills, Behar. *Mem. Geol. Surv. India Palaeontol. Indica* 20(2): 1–19.
- . 1932b. A petrified *Williamsonia* (*W. sewardiana* sp. nov.) from the Rajmahal Hills, India. *Mem. Geol. Surv. India Palaeontol. Indica* 20(3): 1–19.
- . 1948. The Pentoxyleae: a new group of Jurassic gymnosperms from the Rajmahal Hills of India. *Bot. Gaz. (Crawfordsville)* 110: 47–80.
- SALMENOVA, K. Z. 1979. Characteristics of Permian flora of southern Kazakhstan and its relations to the adjacent floras. *Paleontol. J.* 1979: 119–127.
- SAMPSON, F. B. & P. K. ENDRESS. 1984. Pollen morphology in the Trimeniaceae. *Grana Palynol.* 23: 129–137.
- SCHABILION, J. T. & N. C. BROTZMAN. 1979. A tetrahedral megaspore arrangement in a seed fern ovule of Pennsylvanian age. *Amer. J. Bot.* 66: 744–745.
- SCHECKLER, S. E. 1978. Ontogeny of progymnosperms. II. Shoots of Upper Devonian Archaeopteridales. *Canad. J. Bot.* 56: 3136–3170.
- & H. P. BANKS. 1971. Anatomy and relationships of some Devonian gymnosperms from New York. *Amer. J. Bot.* 58: 737–751.
- SCHOPF, J. M. 1938. Spores from the Herrin (no. 6) coal bed in Illinois. *Rep. Invest. Illinois State Geol. Surv.* 50: 1–55.
- . 1976. Morphologic interpretation of fertile structures in glossopterid gymnosperms. *Rev. Palaeobot. Palynol.* 21: 25–64.
- SCOTT, A. C. & W. G. CHALONER. 1983. The earliest conifer. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 220: 163–182.
- SCOTT, D. H. 1919. On the fertile shoots of *Mesoxylon* and an allied genus. *Ann. Bot. (London)* 33: 1–21.
- . 1923. *Studies in Fossil Botany. II. Spermatophyta.* Black, London.
- & A. MASLEN. 1910. On *Mesoxylon*, a new genus of Cordaitales—preliminary note. *Ann. Bot. (London)* 24: 236–239.
- SCOTT, R. A. 1960. Pollen of *Ephedra* from the Chinle Formation (Upper Triassic) and the genus *Equisetosporites*. *Micropaleontology* 6: 271–276.
- , E. S. BARGHOORN & E. B. LEOPOLD. 1960. How old are the angiosperms? *Amer. J. Sci.* 258A: 284–299.
- SEWARD, A. C. 1904. Catalogue of Mesozoic plants in the British Museum. The Jurassic Flora, Pt. 1. British Museum (Natural History), London.
- . 1913. A petrified *Williamsonia* from Scotland. *Philos. Trans.* 203: 101–126.
- . 1917. Fossil Plants. III. Pteridospermeae, Cycadofilices, Cordaitales, Cycadophyta. Cambridge Univ. Press, Cambridge.
- SHARMA, B. D. 1969. Further observations on *Williamsonia santalensis* with a description of a new species. *Palaeontographica, Abt. B, Paläophytol.* 125: 93–103.
- . 1971. On a collection of Bennettitalean stems and fructifications from Amarjola in the Rajmahal Hills, India. *Palaeontographica, Abt. B, Paläophytol.* 135: 48–52.
- . 1974. Ovule ontogeny in *Williamsonia* Carr. *Palaeontographica, Abt. B, Paläophytol.* 148: 137–143.
- SINGH, H. 1978. Embryology of gymnosperms. *Handb. Pflanzenanat.* 10(2): 1–302.
- SITHOLEY, R. V. & M. N. BOSE. 1953. *Williamsonia santalensis* sp. nov. A male fructification from the Rajmahal Series with remarks on the structure of *Ortheanthus polyandra* Ganju. *Palaeobotanist* 2: 29–39.
- & ———. 1971. *Weltrichia santalensis* (Sith. & Bose) and other bennettitalean male fructifica-



- tions from India. *Palaeontographica*, Abt. B, Paläophytol. 131: 151–159.
- SMITH, D. L. 1964. The evolution of the ovule. *Biol. Rev. Cambridge Philos. Soc.* 39: 137–159.
- SMOOT, E. L., R. K. JANSEN & T. N. TAYLOR. 1981. A phylogenetic analysis of land plants: a botanical commentary. *Taxon* 30: 65–67.
- SPORNE, K. R. 1970. *The Morphology of Pteridophytes*, 3rd edition. Hutchinson, London.
- . 1971a. *The Morphology of Gymnosperms*. Hutchinson, London.
- . 1971b. *The Mysterious Origin of Flowering Plants*. (Oxford Biology Readers, no. 3.) Oxford Univ. Press, Oxford.
- . 1974. *The Morphology of Angiosperms*. Hutchinson, London.
- SRIVASTAVA, S. C. 1973. A new microsporangiate fructification from the Triassic of Nidpur, India. *Palaeobotanist* 22: 19–22.
- . 1974. Pteridospermic remains from the Triassic of Nidpur, Madhya Pradesh, India. *Geophytology* 4: 54–59.
- STEBBINS, G. L. 1974. *Flowering Plants: Evolution Above the Species Level*. Harvard Univ. Press, Cambridge.
- STEEVES, M. W. & E. S. BARGHOORN. 1959. The pollen of *Ephedra*. *J. Arnold Arbor.* 40: 221–255.
- STERLING, C. 1963. Structure of the male gametophyte in gymnosperms. *Biol. Rev. Cambridge Philos. Soc.* 38: 167–203.
- STEVENS, P. F. 1980. Evolutionary polarity of character states. *Annual Rev. Ecol. Syst.* 11: 333–358.
- . 1981. On ends and means, or how polarity criteria can be assessed. *Syst. Bot.* 6: 186–188.
- . 1984. Homology and phylogeny: morphology and systematics. *Syst. Bot.* 9: 395–409.
- STEVENSON, D. W. 1980. Form follows function in cycads. *Fairchild Trop. Gard. Bull.* 35: 20–24.
- . 1982. Sporophyll vasculature in the Cycadales. *Publ. Bot. Soc. Amer., Misc. Ser.* 162: 25. [Abstract.]
- STEWART, W. N. 1951. A new *Pachytesta* from the Berryville locality of southeastern Illinois. *Amer. Midl. Naturalist* 46: 717–742.
- . 1976. Polystely, Primary Xylem and the Pteropsida. *Birbal Sahni Institute of Paleobotany*, Lucknow.
- . 1983. *Paleobotany and the Evolution of Plants*. Cambridge Univ. Press, New York.
- STIDD, B. M. 1981a. The current status of medullosan seed ferns. *Rev. Palaeobot. Palynol.* 32: 63–101.
- . 1981b. Perspectives on Paleozoic seed ferns: concluding remarks. *Rev. Palaeobot. Palynol.* 32: 123–125.
- STOCKEY, R. A. 1982. The Araucariaceae: an evolutionary perspective. *Rev. Palaeobot. Palynol.* 37: 133–154.
- STOPES, M. C. 1910. Adventitious budding and branching in *Cycas*. *New Phytol.* 9: 235–241.
- . 1918. New Bennettitean cones from the British Cretaceous. *Philos. Trans., Ser. B*, 208: 389–440.
- STRASBURGER, E., H. SCHENK, F. NOLL & A. F. W. SCHIMPER. 1898. *A Textbook of Botany* (translated by H. C. Porter). MacMillan, London.
- SURANGE, K. R. & S. CHANDRA. 1975. Morphology of the gymnospermous fructifications of the *Glossopteris* flora and their relationships. *Palaeontographica*, Abt. B, Paläophytol. 149: 153–180.
- TAKHTAJAN, A. 1969. *Flowering Plants, Origin and Dispersal*. Oliver and Boyd, Edinburgh.
- . 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev. (Lancaster)* 46: 225–359.
- TAYLOR, T. N. 1965. Paleozoic seed studies: a monograph of the American species of *Pachytesta*. *Palaeontographica*, Abt. B, Paläophytol. 117: 1–46.
- . 1973. A consideration of the morphology, ultrastructure and multicellular microgametophyte of *Cycadeoidea dacotensis* pollen. *Rev. Palaeobot. Palynol.* 16: 157–164.
- . 1978. The ultrastructure and reproductive significance of *Monoletes* (Pteridospermales) pollen. *Canad. J. Bot.* 56: 3105–3118.
- . 1981a. *Paleobotany. An Introduction to Fossil Plant Biology*. McGraw Hill, New York.
- . 1981b. Pollen and pollen organ evolution in early seed plants. Pp. 1–25 in K. J. Niklas (editor), *Paleobotany, Paleoecology and Evolution*, 2. Praeger, New York.
- . 1982. Ultrastructural studies of Paleozoic seed fern pollen: sporoderm development. *Rev. Palaeobot. Palynol.* 37: 29–53.
- & C. P. DAGHLIAN. 1980. The morphology and ultrastructure of *Gothania* (Cordaiales) pollen. *Rev. Palaeobot. Palynol.* 29: 1–14.
- & M. A. MILLAY. 1981. Morphologic variability of Pennsylvanian lyginopterid seed ferns. *Rev. Palaeobot. Palynol.* 32: 27–62.
- & G. W. ROTHWELL. 1982. Studies of seed fern pollen: development of the exine in *Monoletes* (Medullosales). *Amer. J. Bot.* 69: 570–578.
- , M. A. CICHAN & A. M. BALDONI. 1984. The ultrastructure of Mesozoic pollen: *Pteruchus dubius* (Thomas) Townrow. *Rev. Palaeobot. Palynol.* 41: 319–327.
- THODAY, M. G. 1911. The female inflorescence and ovules of *Gnetum africanum*, with notes on *Gnetum scandens*. *Ann. Bot. (London)* 25: 1101–1135.
- & E. M. BERRIDGE. 1912. The inflorescences and flowers of *Ephedra*. *Ann. Bot. (London)* 26: 953–985.
- THOMAS, H. H. 1925. The Caytoniales, a new group of angiospermous plants from the Jurassic rocks of Yorkshire. *Philos. Trans.* 213: 299–363.
- . 1933. On some Pteridospermous plants from the Mesozoic Rocks of South Africa. *Philos. Trans.* 222: 193–265.
- . 1955. Mesozoic Pteridosperms. *Phytomorphology* 5: 177–185.
- . 1958. *Lidgettonia*, a new type of fertile *Glossopteris*. *Bull. Brit. Mus. (Nat. Hist.), Geol.* 3: 179–189.
- & N. BANCROFT. 1913. On the cuticles of some recent and fossil cycadean fronds. *Trans. Linn. Soc. London, Bot.* 8: 155–204.
- THOMPSON, W. P. 1916. The morphology and affinities of *Gnetum*. *Amer. J. Bot.* 4: 135–184.
- . 1918. Independent evolution of vessels in Gnetales and angiosperms. *Bot. Gaz. (Crawfordsville)* 71: 314–326.
- THOMSON, R. B. 1905. The megaspore-membrane of



- the gymnosperms. Univ. Toronto Stud., Biol. Ser. 4: 1–64.
- TIDWELL, W. D., A. D. SIMPER & G. F. THAYN. 1977. Additional information concerning the controversial Triassic plant: *Sanmiguelia*. *Palaeontographica*, Abt. B, Paläophytol. 163: 143–151.
- TOMLINSON, P. B. 1984. [Review of:] C. B. Beck, R. Schmid & G. W. Rothwell. Stelar morphology and the primary vascular system of seed plants. *Taxon* 33: 143–145.
- TOWNROW, J. A. 1960. The Peltaspermaeae, a pteridosperm family of Permian and Triassic age. *Palaeontology* 3: 333–361.
- . 1962a. On *Pteruchus* a microsporophyll of the Corystospermaceae. *Bull. Brit. Mus. (Nat. Hist.)*, Geol. 6: 287–320.
- . 1962b. On some disaccate pollen grains of Permian to Middle Jurassic age. *Grana Palynol.* 3: 13–44.
- . 1965. A new member of the Corystospermaceae Thomas. *Ann. Bot. (London)* n.s. 29: 495–511.
- TRALAU, H. 1968. Evolutionary trends in the genus *Ginkgo*. *Lethaia* 1: 63–101.
- TREVISAN, L. 1980. Ultrastructural notes and considerations on *Ephedripites*, *Eucommiidites* and *Monosulcites* pollen grains from Lower Cretaceous sediments of southern Tuscany (Italy). *Pollen & Spores* 22: 85–132.
- TRIVETT, M. L. V. C. 1983. Pollen cones of a mesarchordaitean from the Upper Pennsylvanian of the Appalachian Basin. *Amer. J. Bot.* 70(5,2): 81. [Abstract.]
- & G. W. ROTHWELL. 1985. Morphology, systematics and paleoecology of Palaeozoic fossil plants: *Mesoxylon priapi* sp. nov. (Cordaitales). *Syst. Bot.* 10: 205–223.
- UPCHURCH, G. R., JR. 1984. Cuticular anatomy of angiosperm leaves from the Lower Cretaceous Potomac group. I. Zone I leaves. *Amer. J. Bot.* 71: 192–202.
- & P. R. CRANE. 1985. Probable gnetalean megafossils from the Lower Cretaceous Potomac Group of Virginia. *Amer. J. Bot.* 72(6): 903. [Abstract.]
- VAKHRAMEEV, V. A. & V. A. KRASSILOV. 1979. Reproductive organs of a shoot of a flowering plant from the Albion of Kazakhstan. *Paleontol. Zurn.* 1979: 121–128.
- VAN CAMPO, M. & B. LUGARDON. 1973. Structure grenue infratectale de l'ectexine des pollens de quelques Gymnospermes et d'Angiospermes. *Pollen & Spores* 15: 171–187.
- VISHNU-MITRE. 1953. A male flower of the Pentoxyleae with remarks on the structure of the female cones of the group. *Palaeobotanist* 2: 75–84.
- VORONIN, N. S., N. B. VORONKINA & M. M. LODKINA. 1973. Structure of the root apex in Gnetales. *Bot. Zurn. (Moscow & Leningrad)* 58: 1589–1596. [In Russian.]
- WALKER, J. W. 1974a. Evolution of exine structure in the pollen of primitive angiosperms. *Amer. J. Bot.* 61: 891–902.
- . 1974b. Aperture evolution in the pollen of primitive angiosperms. *Amer. J. Bot.* 61: 1112–1137.
- . 1976. Comparative pollen morphology and phylogeny of the Ranalean complex. Pp. 241–299 in C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- & J. A. DOYLE. 1975 [1976]. The bases of angiosperm phylogeny: palynology. *Ann. Missouri Bot. Gard.* 62: 664–723.
- & A. G. WALKER. 1984 [1985]. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. *Ann. Missouri Bot. Gard.* 71: 464–521.
- WATROUS, L. E. & Q. D. WHEELER. 1981. The out-group comparison method of character analysis. *Syst. Zool.* 30: 1–11.
- WETTSTEIN, R. 1935. *Handbuch der Systematischen Botanik*, 4th edition. F. Deuticke, Leipzig and Vienna.
- WHITE, M. E. 1978. Reproductive structures of the Glossopteridales in the plant fossil collection of the Australian Museum. *Rec. Austral. Mus.* 31: 473–505.
- . 1981. Revision of the Talbrager Fish Bed flora (Jurassic) of New South Wales. *Rec. Austral. Mus.* 33: 695–721.
- WIELAND, G. R. 1906. American Fossil Cycads. Structure. *Publ. Carnegie Inst. Wash.* 34(1): 1–296.
- . 1916. American Fossil Cycads. Volume 2. Taxonomy. *Publ. Carnegie Inst. Wash.* 34(2): 1–277.
- WILDE, M. H. 1944. A new interpretation of coniferous cones. I. Podocarpaceae (*Podocarpus*). *Ann. Bot. (London)* n.s. 8: 1–41.
- WILEY, E. O. 1979. Ancestors, species and cladograms—remarks on the symposium. Pp. 211–244 in J. Cracraft & N. Eldredge (editors), *Phylogenetic Analysis and Paleontology*. Columbia Univ. Press, New York.
- . 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. Wiley and Sons, New York.
- WODEHOUSE, R. P. 1935. *Pollen Grains*. McGraw-Hill, New York.
- . 1936. Evolution of pollen grains. *Bot. Rev. (Lancaster)* 2: 67–84.
- WOLFE, J. A., J. A. DOYLE & V. M. PAGE. 1975 [1976]. The bases of angiosperm phylogeny: paleobotany. *Ann. Missouri Bot. Gard.* 62: 801–824.
- WORDSELL, W. C. 1906. The structure and origin of the Cycadaceae. *Ann. Bot. (London)* 20: 129–159.
- YOUNG, D. A. 1981. Are the angiosperms primitively vesselless? *Syst. Bot.* 6: 313–330.
- & P. M. RICHARDSON. 1982. A phylogenetic analysis of extant seed plants: the need to utilize homologous characters. *Taxon* 31: 250–254.
- ZAVADA, M. S. 1984 [1985]. Angiosperm origins and evolution based on dispersed fossil pollen ultrastructure. *Ann. Missouri Bot. Gard.* 71: 444–463.